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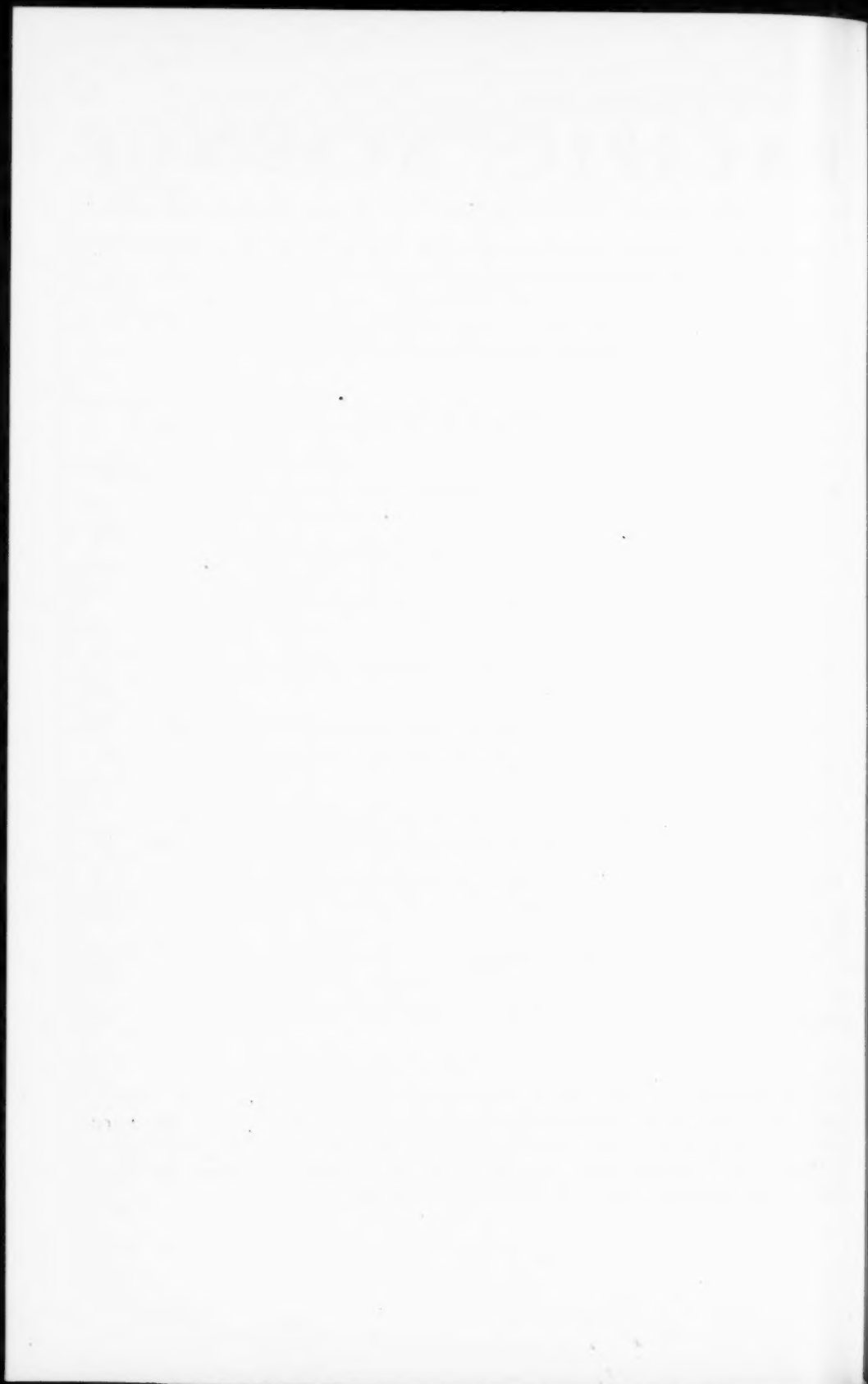
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## The Flora of Australia as a Measure of the Antiquity of the Angiosperms

KARL SUESSENGUTH<sup>1</sup>

### INTRODUCTION

IF ONE INTENDS to consider as difficult a problem as the early history of a large land area, Australia would seem to be particularly suitable for such a study: its long geographic isolation and the great number of scientific investigations to which it has been subjected make it a natural choice.

Australia's land connection with the island groups of Malaysia (except for New Guinea) was ended in the Upper Cretaceous period. According to physicists' calculations, based on the rates of disintegration of radioactive elements, about 30-40 million years have passed since the Eocene epoch in early Cenozoic time. Inasmuch as the Upper Cretaceous period occurred before the Eocene epoch, it can be concluded that, on the whole, the Australian flora and fauna have remained undisturbed for an extremely long time. Under these circumstances of isolation, ancient forms of plant and animal life have been preserved, while, during the long periods since the isolation began, new species of plants and animals have developed from them as well. It must not be forgotten, however, that immigration also has occurred, introducing new species into Australia's plant and animal life since the beginning of its geographic isolation.

The many investigations into the animal life of Australia have given unequivocal evidence of the continent's isolation. Today the most primitive mammals—the Monotremata (*Ornithodelphia*) and the species of *Echidna*, *Proechidna*, and *Ornithorhynchus*—appear

only in Australia and in New Guinea. These mammals resemble reptiles more than any of the other mammals because they lay eggs, have a cloaca, and still possess the number of shoulder bones of primitive animals. As fossil evidence has shown, their ancestors appeared during the Triassic formation, to become, in fact, the first of the mammals. They increased in number during the Jurassic period, but, to a great extent, they died out as early as the Eocene epoch. In Australia, however, some of these primitive mammals have survived to this day, affording us illustration of the concept of "endemism by conservation."

The marsupials, too, are notably typical of Australia. They are not limited to Australia, for there are opossums in North and South America, and Chironectides in South America; but the great majority of the marsupials is found only in Australia. They have developed there, it is interesting to observe, in a manner analogous to the development of placental mammals of the other continents, notably the carnivores, rodents, insectivores, and ungulates.

The survival of the Monotremata and of the Marsupialia can be attributed to the fact that, before man's appearance on the Australian continent, no other placental mammals existed in Australia to prey upon them. There were only mice, which sometimes wandered on driftwood from island to island, and bats; but these were not significant enemies. (It may be possible, of course, that the mice and the bats first arrived in Australia in times subsequent to the Upper Cretaceous period and, therefore, subsequent to the be-

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ginning of Australia's geographic isolation.) As far as the dingo is concerned, it is supposed that aboriginal Austral inhabitants entering Australia from Malaysia were the first to bring this animal to the southern continent.

It is also pertinent to our thesis to note that zoologists believe that some of the opossums (*Caenolestes*) migrated to North America from South America. Fossils of Marsupialia have been found in Europe and in North and South America, an indication that they must have been distributed over vast regions of the earth. The Marsupialia have survived chiefly in Australia, and for this reason Australia today has the oldest and most primitive mammal types in the world.

Now because, geologically speaking, mammals and angiosperms are of about the same age, it is natural to ask if the oldest and most primitive of the flowering plants are also to be found in Australia today. The answer to this question would help us to determine the antiquity of the angiosperms.

This is a question that is difficult to answer, if only because botanists are not in agreement on the most primitive species of angiosperms. This one question asks other questions: If the earliest species of angiosperms could be defined, would it be found that they exist preeminently or even exclusively in Australia? Or, if the earliest species cannot be defined, is it possible to determine, from the Australian flora of today, which are the most primitive species of angiosperms that have succeeded in persisting until this time? These are the problems to be investigated in this paper.

#### WHAT ARE THE MOST PRIMITIVE FAMILIES OF THE FLOWERING PLANTS?

As every botanist knows, the question of primitiveness in flowering plants is a controversial one. Some think that certain species of the Monochlamydeae are the most primi-

tive, while others think that the Polycarpiceae among the Choripetales are the most ancient. Once, even certain of the Monocotyledones (the Pandanales) were considered for the distinction, although this claim, of course, could not be proved by any significant arguments. Inasmuch as this is hardly the place for a discussion of the phylogenetic criteria by which plants are judged, the more pertinent portions of my book, *Neue Ziele der Botanik* (1938), are suggested for reference.

If, in our search for the oldest angiosperms, and in our analysis of the Australian flora, we hold the opinion that those families which are put at the head of the Monochlamydeae in the Engler and Prantl system of classification are the ones which show the most primitive characteristics, we should be supported in this assumption by the Casuarinaceae found in Australia. In their original distribution they extended from Sumatra to the Philippines, New Caledonia, and the Fiji archipelago (Diels, 1926), and to Tahiti, the Austral Islands, and the Marquesas (Brown, 1935). As yet, however, there is no reliable basis for the hypothesis that the Casuarinaceae are more nearly related to the Gymnospermae than is any other family of the Angiospermae. Neither can this supposition be proved for the Proteaceae and the Balanopsidaceae, which are also placed at the beginning of the Monochlamydeae in the Engler and Prantl taxonomic system. In Australia more than half of all of the species of Monochlamydeae are Proteaceae (about 600 species), although the family has extended to southern Africa, southern Asia, and South America (Vester, 1940). The species of Proteaceae are almost exclusively ligneous plants, which would indicate that, phylogenetically, they are rather an old group, but in the absence of paleontological evidence we cannot be certain that these species are really older than many others we might consider, so we have to be content only with supposing that they *might* be.



On the other hand, if we hold the opinion, as many botanists do, that the Polycarpicæ are the most primitive of the Angiospermae, we should find that only two very small families of Polycarpicæ are endemic in Australia: the Eupomatiaceae and the Himantandraceae, which are related to the Eupomatiaceae, but which possess neither calyx nor corolla (Diels, 1919: 126 *et seq.*). The other families of Polycarpicæ are not well represented in Australia: the Magnoliaceae afford only 4 species, the Annonaceae 18, the Nymphaeaceae 5, the Ranunculaceae 17, and the Myristicaceae 1. In view of these facts, it cannot be claimed that the Polycarpicæ are the most primitive of angiosperms in Australia and that a comparison with the preservation of the earliest mammals could be made.

This brief appraisal is enough to show that the angiosperms which most botanists consider to be the oldest of flowering plants (Polycarpicæ) do not exist exclusively or pre-eminently in Australia. But in the information we have learned about the Casuarinaceae and the Proteaceae we may have found certain clues which will be of value later when we investigate their degree of primitiveness.

WHICH SPECIES OF ANGIOSPERMS  
PERSISTING IN AUSTRALIA ARE  
THE MOST PRIMITIVE?

Now we can set about answering the second question, inquiring into the conclusions which can be drawn from a study of the history of the Australian flora. At first it may seem questionable in itself to compare the early histories of flowering plants with those of mammals, particularly when it is realized that the conditions governing their migrations were quite different. We assume that those mammals living in Australia during the Upper Cretaceous period have been isolated since that time because of the continent's isolation, and that only rarely have they been joined by later immigrants. Can the same assumption be made for the flower-

ing plants? Or may those various plant species now found in Australia have migrated to the continent since its separation because they—or rather, their seeds—could cross the ocean gap while the animals were not able to do so?

To obtain a general view of the whole flora of Australia, let us consider the catalogue of F. von Mueller, his *Census of Australian Plants* (1889). Because of the recent advances in our knowledge, Mueller's list is neither complete nor infallible, yet it is not likely that the proportions of the numbers of species within large groups and of the endemic species have changed significantly since that time. Therefore we may use the *Census* without hesitation, all the more necessarily because there does not exist a later catalogue for the whole Australian territory (including Tasmania but not New Zealand).

Mueller's catalogue lists 8,842 species, and, because it does not mention those species introduced in recent times (since about 1800), it is well fitted for our purpose. Of these 8,842 species, 7,734 (that is, 87.5 per cent) are endemic in the larger sense of the word—that is to say, they are found in Australia itself but may also extend to New Zealand and to parts of Polynesia as well. The percentage of endemism is extremely high.

Table 1 may serve for comparison of the percentage of endemic plants found in Australia with those found in other parts of the world.

As a matter of fact, it is probable that among the 8,842 species listed in Mueller's *Census of Australian Plants* there may be a great many species which were introduced by man, although this hypothesis cannot be substantiated in its details. If this is true, however, the percentage of endemism in Australia would be even higher than it is here calculated.

There is no doubt but that the longer a country has been isolated the more endemics

TABLE 1  
REPRESENTATION OF ENDEMIC PLANTS IN  
AUSTRALIA AND IN OTHER PARTS  
OF THE WORLD

REGION	APPROXIMATE PERCENTAGE OF ENDEMIC PLANTS	REFERENCE
Australia	87.5	calculated from Mueller, 1889.
New Zealand	73	calculated from Cheeseman, 1925.
Hawaii	90	according to St. John, 1946.
Galapagos	40	calculated from Stewart, 1911.
Sokotra	33	according to Drude, 1896.
Balkans	26	calculated from Ha- yek and Markgraf, 1927-1933, and from Turrill, 1929.
Iceland	0	calculated from Os- tenfeld and Gröntved, 1934.

For statements about smaller islands, see O. Drude, *loc. cit.*

it shows; and we may assume that, other conditions being equal, the percentage of its endemism would enable us to measure the length of its period of isolation. Scandinavia, for example, has very few endemics (and these are "weak" endemics in the systematic sense) because there was not enough time for it to be overgrown with flowering plants be-

fore the sparse soil-cover left by the retreating glaciers was removed by erosion, and because the short period during which alluvial soil has been collecting since glaciation has not been long enough for the development of many new species. It is true, of course, that Scandinavia can hardly be compared with Australia, inasmuch as the prevailing temperatures in Scandinavia are not at all favorable for the formation of new species (Sterner, 1943: 84).

Even if we considered as not being endemic to Australia those plants which are also found in New Zealand and in Polynesia, there remain, nevertheless, 7,501 species, or 84.8 per cent, which are limited to continental Australia and Tasmania. Obviously the reduction in number is a minor one.

An appreciation of the manner of the distribution of endemic species among the larger plant groups of the Australian flora will be gained from Table 2, which shows that among the Angiospermae, at least, the endemic species are quite equally distributed among the three groups into which the angiosperms are divided, with 89.3 per cent for the Sympetalae, 90.2 per cent for the Dialypetalae, and 92.9 per cent for the Monochlamydeae. This high number of endemics is not shared by the Monocotyledones, among which only 79.7 per cent of the species are

TABLE 2  
DISTRIBUTION OF ENDEMIC SPECIES AMONG THE LARGER PLANT GROUPS  
OF THE AUSTRALIAN FLORA

PLANT GROUP	TOTAL NUMBER OF SPECIES IN GROUP	PERCENTAGE OF WHOLE FLORA REPRESENTED BY GROUP	NUMBER OF ENDEMIC SPECIES IN GROUP	PERCENTAGE OF TOTAL NUMBER OF ENDEMIC SPECIES IN GROUP
Pteridophytæ	244	2.7	124	50.8
Gymnospermae	43	0.5	43	100.0
Monochlamydeae	1,130	12.8	1,050	92.9
Dialypetalae	3,641	41.2	3,286	90.2
Sympetalae	2,229	25.2	1,991	89.3
Monocotyledones	1,555	19.6	1,240	79.7
Totals	8,842	100.0	7,734	87.5 of the total number

endemic. Relatively speaking, they show the smallest number of endemics among the angiosperms, which is rather an interesting fact, inasmuch as in the flora of European countries a certain parallel can be found for these values (Schmidt, 1945).

The smaller percentage of endemics among the Pteridophytae may be explained by the fact that the ferns are more readily disseminated over greater distances by means of their spores. It may be that in this manner many species of ferns immigrated into Australia, or emigrated from it, after its geographical isolation had begun. The same supposition is valid for many species of the Gramineae and for the Cyperaceae among the Monocotyledones.

When we consider the great number of endemics present in the Australian flora, we are tempted to jump to the important conclusion that, in later times, only an inconsiderable migration of plants took place into Australia from abroad. If there had been any considerable degree of migration, we should be able to find the species of plants now living in Australia spread over other continents as well, and especially over Malaysia. Actually, however, they are not so widely distributed, but are confined as endemics to Australia. The evidence is such that we may safely conclude, therefore, that a pronounced development of species took place on the Australian continent *after* the geographical isolation had begun. But, if few species have migrated into Australia from abroad over such a very long time (except in the cases of the Pteridophytae, which show the fewest endemics), is it not probable that all of the types which evolved into endemic species were already in existence *before* the period of geographical isolation, that is, during the Upper Cretaceous period? Did the numerous representatives of the characteristic families of the Australian flora already flourish in those ancient times? Was the Australian flora of those days similar, at least in its families,

to the Australian flora as it is now? Above all, did all of the many families of the Australian flora exist then as they do now? These questions are not easy to answer, and before investigating them it will be useful to give a rather detailed account of the Australian flora itself.

To begin with, it must be accepted that the evolution of the *families* of the flowering plants had begun in times earlier than those of the Upper Cretaceous period, for only a very few endemic families are found in Australia, and these have only a very few species in them. These families are the Akaniaceae, Balanopsidaceae (which also appears in New Guinea), Brunoniaceae, Byblidaceae, Cephalotaceae, and Tremandraceae. These are the only families that have developed endemically in Australia since the Upper Cretaceous period, although they might possibly have been preserved in Australia from times even more ancient than the Upper Cretaceous; since that period there has not been time enough for a further evolution of families. From this evidence we can conclude that it is very likely that the primitive ancestral types of the other, much larger, families of the Australian flora existed during the Upper Cretaceous period. If they had immigrated into Australia after Upper Cretaceous time—which is a possibility we naturally have to take into consideration—then they ought to be found in other parts of the world as well. We shall learn later in detail how far this is true. But, in any event, we must not assume that the six endemic Australian families also existed, at one time, in other parts of the world, only to die out later in those places, so that now they are native to Australia alone. We must be cautious with this kind of conclusion, a lesson which has been made obvious by the example of the mammals of New Zealand, referred to by Diels (1897) in his work on the vegetative biology of New Zealand. We shall return to this matter later in this paper.

According to A. Engler (1882), 425 of the 1,393 genera of the Australian flora—that is, 30.5 per cent—are endemic. This is a statement of great importance, for from it we learn that the time interval between the Upper Cretaceous period and the present time has been sufficient for the creation of a great number of new genera—almost a third of the genera found in Australia—or for the conservation in Australia of a part of them while in other continents they have become extinct. It has already been stated that the same suppositions are valid for 90 per cent of all the Australian species. In short, the period from Upper Cretaceous time until the present has been long enough to create, or, exclusively, to conserve, 30.5 per cent of the *genera* and at least 90 per cent of the *species* of the Australian flora. On the other hand, it has not been long enough a time to permit the creation, or the exclusive conservation, of very many of the families of the Australian flora, particularly of the larger families.

It is interesting, for the sake of comparisons not unimportant to the arrival at a conclusion, to see how the species of the larger groups are distributed in other parts of the world. According to Hegi's *Flora* (1906-1931), the larger groups of plants are represented in central Europe—Germany, Austria, and Switzerland—by the numbers presented

in column 1 of Table 3. These figures are converted, in column 2, into percentage values which can be compared with the figures for the same plant groups in Australia (column 3).

In several of these groups—the Pteridophytae, the Gymnospermae, and the Monochlamydeae—the percentage values for Australia do not differ much from those of central Europe. In Australia the Monocotyledones and the Sympetalae appear somewhat less frequently than they do in Europe; while the Dialypetales are found somewhat more frequently in Australia than in central Europe.

In R. Mansfeld's catalogue of ferns and flowering plants (1940), the figures given for that part of central Europe included in Germany, Austria, Bohemia, and Moravia are presented in Table 4.

In northern Europe the Monocotyledones are even more plentiful. In England they form 25.3 per cent of the flora (Druce, 1932); in Iceland and the Faroes, 30.8 per cent (Ostenfeld, 1934); in Greenland, 31.2 per cent (Ostenfeld, 1926); in Novaya Zemlya, 33.3 per cent (Ekstam, 1897); and in Spitzbergen, 31.2 per cent (Nathorst, 1883). In Portugal the Monocotyledones form 20.3 per cent of the flora (Palhinha, 1939); in Italy, 18.6 per cent (Buscalione and Muscatello, 1911-1913); in the Balkans, 16.3 per cent (calculated from Hayek and Markgraf, 1927-1933); and in the territory of the Aegaeen islands, 17.5 per cent (calculated from Reehinger, 1943). It becomes apparent, then, that the number of species of Monocotyledones is greater in northern Europe than it is in southern Europe.

With the Sympetalae quite the opposite representation is found: the northern countries have fewer of these, the southern countries have more: Spitzbergen has 13.5 per cent; Novaya Zemlya, 16.5 per cent; Greenland, 21.1 per cent; the Faroes, 25.5 per cent; England, 25.4 per cent; Germany, 29.5

TABLE 3  
REPRESENTATION OF ENDEMIC SPECIES AMONG  
THE LARGER PLANT GROUPS OF CENTRAL  
EUROPE AND AUSTRALIA

PLANT GROUP	NUMBER OF SPECIES*	PERCENTAGE OF "HIGHER FLORA"	COMPARABLE FIGURES FOR AUSTRALIA
Pteridophytae	74	2.3	2.8
Gymnospermae	11	0.3	0.5
Monochlamydeae	355	11.2	12.8
Dialypetalae	1,043	32.9	41.2
Sympetalae	1,042	32.8	25.2
Monocotyledones	648	20.4	17.6

\* According to Hegi (1906-1931).

TABLE 4  
REPRESENTATION OF ENDEMIC SPECIES AMONG THE LARGER PLANT GROUPS OF CENTRAL  
EUROPE, THE AEGEAN ISLANDS, AND PORTUGAL

PLANT GROUP	CENTRAL EUROPE*		AEGEAN ISLANDS†		PORTUGAL‡	
	NUMBER OF SPECIES	PERCENTAGE OF HIGHER FLORA	NUMBER OF SPECIES	PERCENTAGE OF HIGHER FLORA	NUMBER OF SPECIES	PERCENTAGE OF HIGHER FLORA
Pteridophytae	73	2.3	41	1.2	51	1.9
Gymnospermae	12	0.4	18	0.5	12	0.4
Monochlamydeae	332	10.4	368	11.2	305	11.0
Dialypetalae	1,119	35.2	1,154	35.0	994	36.0
Sympetalae	998	31.4	1,138	34.6	843	30.5
Monocotyledones	645	20.3	574	17.5	557	20.2
Totals	3,179		3,293		2,762	

\*According to Mansfeld (1940). The unimportant differences between Hegi's figures and Mansfeld's may be ascribed to differences in criteria for the recognition of species as well as to the fact that Hegi's *Flora* included Switzerland and the South Tyrol while Mansfeld's did not.

†In his *Flora Aegaea*, Reehinger (1943) covers the territory of the Aegaeian islands from Chalkidike in the north to Rhodes and Candia in the south.

‡The figures for Portugal are given by Ruy Telles Palhinha in his *Flora de Portugal* (1939).

per cent; Portugal, 30.5 per cent; Switzerland, 30.5 per cent; France, 31.2 per cent; Tyrol (including South Tyrol), 33.7 per cent; the Aegaeian islands, 34.6 per cent; Italy, 35.7 per cent; the Balkan countries, 37.4 per cent. (These calculations are taken from A. Schmidt, 1944.)

When the figures for the endemics of Australia are compared with the figures for those parts of Europe which are rich in endemic plants, the contrasts are even more pronounced (Table 5).

From these comparisons we learn that endemic species of the Sympetalae are much more numerous in southern Europe than they are in Australia, and that, at the least, the centers of development of the polyphyletic Sympetalae are not likely to have been located in Australia. If they had been, the percentages of representation would have been reversed.

#### NUMBERS OF SPECIES IN FAMILIES

According to Mueller's figures (1889), which are approximately correct even today, the most important families in Australia,

with respect to the numbers of their species, are these:

FAMILY	NUMBER OF SPECIES
Leguminosae . . . . .	1,065
Myrtaceae . . . . .	663
Proteaceae . . . . .	597
Compositae . . . . .	539
Cyperaceae . . . . .	380
Gramineae . . . . .	345
Epacridaceae . . . . .	275
Orchidaceae . . . . .	272
Euphorbiaceae . . . . .	226
Goodeniaceae . . . . .	220
Rutaceae . . . . .	190

These eleven families, with a total of 4,372 species, include more than half of all the Australian phanerogams, of which there are 8,555 species. It is worth noting how remarkably the Leguminosae, Myrtaceae, Compositae, and Orchidaceae have developed. As we know, these families are by no means primitive. In this way the plants of the present Australian flora give evidence that their ancestors (related systematically) must have been well-developed at the time of the Upper Cretaceous period and even before.

The percentages of the endemic species in these 11 Australian families are tabulated as follows:



FAMILY	PERCENTAGE OF ENDEMIC SPECIES IN AUSTRALIA
Proteaceae . . . . .	100
Epacridaceae . . . . .	100
Goodeniaceae . . . . .	99.9
Myrtaceae . . . . .	98.3
(including all Leptospermoideae-Chamaelaucieae, all Leptospermoideae-Leptospermeae-Calothamninae, and all Leptospermoideae-Backhousiinae)	
Rutaceae . . . . .	97.4
Orchidaceae . . . . .	94.8
Compositae . . . . .	91.5
Leguminosae . . . . .	90.6
(including all Papilionaceae-Genisteae-Bossiacinae)	
Euphorbiaceae . . . . .	88.0
Cyperaceae . . . . .	70.3
Gramineae . . . . .	69.3

Of the larger families, 13 have only one species which has extended its range beyond Australia to other countries; these families are listed here, together with the number of species in each family which are found only in Australia:

FAMILY	NUMBER OF SPECIES IN AUSTRALIA
Myoporaceae . . . . .	76
Haemodoraceae . . . . .	66
Restionaceae . . . . .	93
Dilleniaceae . . . . .	95
Saxifragaceae . . . . .	35
Magnoliaceae . . . . .	18
Tremandraceae . . . . .	17
Annonaceae . . . . .	16
Stackhousiaceae . . . . .	13
Coniferae . . . . .	29
Cycadaceae . . . . .	14
Casuarinaceae . . . . .	24
Pittosporaceae . . . . .	40

The Chenopodiaceae, with 111 species in Australia; the Hallorhagidaceae, with 58 species in Australia; and the Santalaceae, with 43 species in Australia, each has only two species which extend beyond the continent, and the Amaranthaceae, with 100 Australian species, has five species which extend their range beyond Australia to New Zealand and Polynesia. Of the smaller families, many have species appearing in territories other than the Australian, and are therefore without value in evaluating endemism in Australia:

FAMILY	NUMBER OF SPECIES IN AUSTRALIA	OUTSIDE AUSTRALIA
Nymphaeaceae . . . . .	5	4 or 5
Guttiferae . . . . .	4	3
Geraniaceae . . . . .	8	5
Convolvulaceae . . . . .	70	33
Lythraceae . . . . .	19	12
Onagraceae . . . . .	5	3
Rhizophoraceae . . . . .	7	7
Cucurbitaceae . . . . .	28	13
Hydrocharitaceae . . . . .	9	7
Lemnaceae . . . . .	6	6
Najadaceae	} . . . 36	20
Potamogetonaceae		
Aponogetonaceae		

Many others of the smaller families might be added to this list, to support this contention.

#### THE PHYLOGENETIC AGE OF SYSTEMATIC GROUPS

Let us turn now to another question which is more easily answered: Do there exist, among the families of Australian plants, any

TABLE 5  
COMPARISON OF PERCENTAGES OF ENDEMIC SPECIES IN THE HIGHER PLANT GROUPS OF AUSTRALIA WITH THOSE OF SOUTHERN EUROPE

PLANT GROUP	AUSTRALIA	ITALY	THE BALKANS	SARDINIA
Pteridophytae	1.6	0.5	0.0	4.2
Gymnospermae	0.5	0.0	0.2	0.0
Monochlamydeae	13.6	2.0	11.8	0.0
Dialypetalae	42.5	35.1	28.8	29.8
Sympetalae	25.8	56.4	49.9	55.3
Monocotyledones	16.0	5.9	9.3	10.6

of the larger systematic groups which are of very ancient age? The criteria for the recognition of phylogenetically old and new characteristics have been treated at length in my book (Suessenguth, 1938: 19 *et seq.*).

Let us consider the Leguminosae first. Among the members of the subfamily Mimosoideae the most important genus in Australia is *Acacia*, which has more than 300 Australian species. The rest of the genera of the Mimosoideae in Australia number only about 23 species.

Is the genus *Acacia*, then, an old or a new genus among the Mimosoideae? If we accept the general phylogenetic principle that free stamens are more primitive than fused stamens, and if we agree that the group of species with numerous stamens (now classified in the tribes Ingeae and Acacieae) is older than the group of species which have 10 or fewer than 10 stamens (now classified in the tribes Eumimoseae, Adenanthereae, Piptadenieae, and Parkieae), then we must conclude that the species of the tribe Acacieae, with their free stamens, are more primitive than are the more or less synanthrous species of the tribes Ingeae and Parkieae. The Acacieae, with the genus *Acacia*—in which the filaments are free or only grown together to form a short ring—are undoubtedly the most primitive of the Mimosoideae, and apparently the plants of the genus *Acacia* are the most primitive of all of the Acacieae. Therefore, Australia shows the greatest number of oldest types among the Mimosoideae.

The subfamily Papilionatae presents much the same evidence. The most primitive tribes of the Papilionatae are those which have free stamens—the Sophoreae and the Podalyrieae. The Sophoreae generally have pinnate leaves, while the Podalyrieae have simple or digitate, rarely pinnate, leaves. Because of their simple leaves, the Podalyrieae may be considered the more primitive tribe. The Podalyrieae number 350 species in Australia, while

all of the other tribes of Papilionatae are far less numerous.

In summary, as far as the Leguminosae are concerned, it can be said that the Mimosoideae and the Papilionatae show the most pronounced development of primitive species in Australia.

Among the tribes of the Labiatae, the Prostanthereae are by far the most numerous in Australia, having 89 species compared with 31 for all of the other tribes. If we study the subfamilies of the Labiatae, as they are considered by Briquet (in Engler and Prantl, 1897), we come to the conclusion that the most primitive species must be those having no gynobasic pistil—the members of the tribes Ajugoideae and Prostantheroideae. When we investigate these two groups we learn that the Prostantheroideae have ovules with endosperm, while the Ajugoideae do not show any endosperm in their seeds—evidence that the Prostantheroideae are the most primitive of the Labiatae. These primitive Prostantheroideae are confined exclusively to Australia.

Among the Myrtaceae we think that the subfamily having dry fruits—the Leptospermoideae—is the most primitive. In Australia there are about 596 of these species with dry fruits, compared with only 41 species of Myrtoideae which bear berries. In Australia, then, the older subfamily has about 14.5 times as many species as does the younger one. The proportion of Leptospermoideae to Myrtoideae in the rest of the world is quite different: there are 678 species of Leptospermoideae and 1,932 species of Myrtoideae, a ratio of 1:2.85.

Among the Rutaceae the most primitive species are placed in the subfamilies which are inclined to apocarpy rather than in the subfamilies with united carpels (e.g., the Flindersioideae, Spathelioideae, Toddalioidae) or in those with bacciform fruits (e.g., the Aurantioideae). The Rutoideae show a tendency to apocarpy, and among their subfamilies several groups have developed: (a)



those with dorsiventral flowers (the American Cuspariaceae); (b) those without endosperms (the African Diosmeae); (c) those having herbaceous or suffruticose habit (the Ruteae of the northern temperate zone); and (d) those species with doubly digitate leaves (the Dictyolomeae of tropical South America). The remaining tribes of the Rutoideae are the Xanthoxyleae and the Boronieae. The Xanthoxyleae have a tendency to produce unisexual flowers, a characteristic which, for this group, is regarded as a derived feature. The most primitive types of the Rutaceae, then, are probably the Boronieae, and these types are limited to Australia and New Caledonia. In Australia there are about 143 species of the Boronieae and 26 species of the Xanthoxyleae, but only 9 species of the Flindersiaceae, 7 of the Aurantieae, and 3 of the Toddalieae. These figures, which could readily be supplemented with more evidence, show clearly enough that the primitive Rutaceae appear nowhere as plentifully as they do in Australia.

In considering the Loranthaceae, Engler (1894) mentions the Lorantheae as the first state of development and the Viscoideae as the secondary one. The most primitive of the Lorantheae are non-parasitic trees which have no berries—members of the genera *Nuytsia* and *Gaiadendron*. The species of *Nuytsia*, with dry false fruits, are considered more primitive than the species of *Gaiadendron*, with drupe-like false fruits. The species of *Nuytsia* are found only in western Australia. Of the four species of *Gaiadendron*, three are found in the Andes from Peru to Colombia, and one is found in eastern Australia.

Among the Dilleniaceae, two of the subfamilies, the Actinidioideae and the Saurauioideae, show a derived feature in the fusion of their carpels and further development in that the Actinidioideae and most of the Saurauioideae bear real berries. Neither of these subfamilies is represented in the Australian

flora, the Actinidioideae being found in Japan, China, Manchuria, and the Himalayas, while the Saurauioideae are found in tropical Asia and America. All of the Australian species of the Dilleniaceae belong to the more primitive subfamily, the Dillenioidae. One of the tribes of the Dillenioidae, the Acrotremeae, is found outside of Australia, in India and Ceylon; but this is a less primitive tribe than is the Australian one, showing a number of derived characteristics, such as united carpels, a bushy habit, and pinnatifid leaves. The other tribes of Dillenioidae—the Tetracereae, Hibbertieae, and Dilleniaceae—which also have representatives in southern Asia and tropical America, are not well enough known at present for a decision concerning the degree of their primitiveness or evolution.

Among the Restionaceae, the Diplantheae have dithecic anthers and the Haplanthereae have monotheccic anthers. Naturally, those genera with dithecic anthers are regarded as being the more primitive. They appear only in southwestern Australia; the genus *Anarthria*, with free anthers and a trilobular ovary, is the most primitive of them all. Among the Haplanthereae no differentiation can be made upon phylogenetic characteristics, for here the Australian and the African species share some characteristics. Nevertheless, the most primitive representatives do not appear outside of Australia.

The Centrolepidaceae show quite a similar relationship: among them, too, the species with dithecic anthers are also the more primitive ones. They are represented by the genus *Juncella* in southern Australia and in Tasmania.

The Goodeniaceae, although not completely endemic, have most of their representation in Australia. The most primitive genus in the family is *Calogyne*, which has bifid or trifid pistils. Two species of the genus are found in Australia and the third in south China.

Of the seven tribes of the family Proteaceae, the Persoonieae is the most primitive, as Engler has stated in his *Natürliche Pflanzenfamilien* (III/1: 127). The Persoonieae are found in Australia, Tasmania, New Caledonia, and, to a lesser extent, in New Zealand. One species of *Brabeium* appears at the Cape of Good Hope, but has developed farther than its relatives in Australia, as is proved by its floral axis which shows a cyathiform excrescence at the base. In any event, the most primitive representatives of the Proteaceae are almost completely limited to Australia.

In the Santalaceae, the members of the tribe Antholobeae, with their superior ovary, are considered primitive. The genus *Antholobus* is native to Australia. A closely related genus, *Exocarpus*, is found in Australia, Norfolk Island, the Malaysian islands, India, Madagascar, and Hawaii, although most of its species are native to Australia. The genus *Champereia* is found in Malacca and the Malaysian archipelago. It can be concluded, therefore, that the Santalaceae are of Australian-Malaysian—that is to say, of post-Gondwanesian—origin.

The most primitive Apocynaceae are those in which the stamens are not tightly connected with their stigma heads. These are the Plumierioideae, especially a subgroup of them, the Pleiocarpeae, which have apocarpic ovaries, pistils split at the base, and more than two carpels. Among them are two genera with the primitive arrangement of alternate leaves: *Notonerium* Benth., an ericoid bush growing in southern Australia, and *Lepinia* Decne., a tall tree found in Tahiti. The most primitive species of the Apocynaceae, therefore, are Australian-Pacific in their origin.

It might be noted in passing that this same conclusion cannot be drawn for the Asclepiadaceae. Here the Periploceae are the most primitive forms, judging by their tetrad pollen, the translators of which have no retinacula; and of these primitive Periploceae,

the most primitive are those which possess no corona, as, for example, the *Gymnolaima* of Kilimanjaro, Africa, the *Phyllanthera* of Java, and the *Pentamera* of Sumatra. The Asclepiadaceae are generally more highly evolved than are the Apocynaceae, but they do not originate in Australia.

Let us now go on to consider a rather complicated group, the Cyperaceae. Here the species of Scirpoideae, with their hermaphroditic flowers, are more primitive than are the Caricoideae, the flowers of which are rarely hermaphroditic. The nature of the axes in the inflorescences of the Caricoideae also proves to be a derived feature. Among the Scirpoideae there is a tribe, the Hypolytreae, whose members have bracted flowers; and the transverse arrangement of these bracts (as occurs among the Hypolytrinae) might be a more primitive characteristic than is the possession of one or two median bracts (as occurs among the Lipocarphinae). Among the Hypolytrinae the genus *Hypolytrum*, whose species show free bracts, is most primitive. A species of *Hypolytrum*, *H. latifolium* L. C. Rich., is found in Queensland, but it is also found in south Asia, Africa, America, and Polynesia. Two species of *Lipocarpa* also have an extensive range. The genus *Hypolytrum* has its representatives in the tropical and subtropical ranges of both hemispheres. All of this evidence would seem to show that the oldest living types of Cyperaceae—which is considered a rather "modern" family—have their native habitat in the tropics, but by no means in Australia.

In contrast to this, the oldest genus of the Scirpoideae-Cyperinae, the genus *Carppha* R. Br.—without disk, but with setaceous involucre, six setae, and a three-cleft pistil—is represented by one species from Australia and New Zealand and by another in extra-tropical Andean South America.

In the large subfamily of the Caricoideae, the Rhynchosporae are the most primitive, inasmuch as, in most cases, they have three

anthers and an involucre. If we except the genus *Oreobolus*—which is somewhat in a special position because of its circum-Pacific distribution and its single, terminal, one-flowered false spikelets (Suessenguth, 1942)—we note that genera with alternate or very slightly distichous bracteal scales are more primitive than are those with distichous scales. Among these genera the most primitive are those which have three style branches and an involucre; of these genera three are especially worthy of consideration here:

*Lepidosperma*, with nine-tenths of its species found in Australia, two in New Zealand, and two in tropical east Asia

*Tricostularia*, with five-sevenths of its species found in Australia, one in Borneo, and one in Ceylon

*Decalepis*, with one species found at the Cape of Good Hope in South Africa.

From this evidence we see that—again if we except the genus *Oreobolus*, which is of old-Pacific origin and which is difficult to classify—most of the oldest types of the Caricoideae are to be found in Australia, while the most primitive species of the whole family of the Cyperaceae are found in the tropics.

In order to complete the picture we should consider some of the families, the origin of which cannot be traced to Australia.

Of the Anacardiaceae the most primitive genus is *Buchanania*, native to tropical Asia, especially to the Malaysian territory, and to northern Australia. The most primitive species of *Buchanania* have four to six free carpels, of which one is fertile.

The Compositae are impossible to trace to their origin, or to differentiate into their most primitive groups, even if we exclude from consideration the tribes which are obviously derived, like the Liguliflorae and the Mutisieae.

The family Cucurbitaceae is divided into the Fevilleae and the Fevillinae. The Fevilleae are the more primitive, having five free anthers and loculamenta which are not grown

together to form a circular ring (except for the slightly more developed Gomphogyninae and the Zanoninae, which have unilocular ovaries). The Fevillinae have trilocular ovaries, and, of course, are more highly evolved than are the Fevilleae. All of these plants are native to tropical America, Brazil, and the West Indies.

Among the Orchidaceae, the more primitive species (the Diandrae-Apostasiinae) are not found in Australia. Species of the genus *Newwiedia*, which have three fertile stamens, appear in Malacca and the Malaysian archipelago; those of the genus *Apostasia*, which have two fertile stamens, appear in the East Indies, the Malaysian archipelago, and tropical Australia. From this it is evident that the oldest types of the whole family belong to the tropics and are found today in territories lying north of Australia.

The distribution of the Piperaceae (as, indeed, of many another smaller family), leads us to expect a tropical origin for them.

Of the Rubiaceae, the more primitive subfamily is that of the Cinchonoideae, whose species have many seeds in each locule of the ovary. Among the Cinchonoideae, the Cinchoninae are more primitive because of their dry fruits. More highly developed groups, like the Condamineae and, to some extent, the Rondeletieae, have radiate flowers which are single or in panicles (but not in clusters), apterous seeds, whole or bipartite stipules, and the habit of trees or shrubs. The Rondeletieae, however, show imbricated or contorted veneration of the corolla, and the contorted veneration, at least, is a derived feature. Among the Condamineae the most primitive species are those in which the sepals are of equal size and in which the petals are simply valvate and not reduplicatively valvate.

The simply valvate species are placed in the genera *Condaminea* (found in Andean South America), *Chimarrhis* (found in Andean South America and in the Antilles),

*Rustia* (from Central America to Brazil), and *Tresanthera* (in Venezuela and in the West Indies). None of these genera even so much as appears in Australia. The reduplicate valvate species of the Condamineae are placed in the genera *Portlandia* (found in the West Indies and in Mexico), *Isidorea* (in Haiti and Cuba), *Bikkia* (from the Pacific islands, New Caledonia, and Malacca), and *Morrierina* (found in New Caledonia).

Of the Rondeletieae, the simpler species, in which there is no contorted vernation of the corolla and in which the petals are not evolved into showy organs, are placed in the genera *Rhachicallis* (found in the Antilles), *Bathysa* (found in Brazil), and *Rondeletia* (found in the Antilles, Central America, and the northern parts of South America).

All of this evidence proves that the Rubiaceae did not originate in Australia, but primarily in the tropical regions of Central and South America and in the West Indies, and only in lesser part in the regions of New Caledonia and the Moluccas.

The most primitive species of the Valerianaceae appear on the Asiatic mainland: Species of *Nardostachys*, with four stamens and the clearly five-parted edge of the calyx, are found in the central Himalayas; species of *Patrinia*, with four stamens, extend westward from Japan through central Asia to the Ural mountains and northward into Arctic territory.

Now, in recapitulation, let us list all the larger systematic groups of the angiosperms, the most primitive types of which are found in Australia: Labiatae, Mimosoideae, Papilionatae, Myrtaceae (sub-family Leptospermoideae), Rutaceae, Santalaceae, Apocynaceae, Goodeniaceae, Proteaceae, Restionaceae, Centrolepidaceae, Loranthaceae, Dilleniaceae, Cyperaceae (subfamily *Caricoideae*). This summary and all of the evidence leading up to it are of great importance for the proper evaluation of many of the problems and questions in the science of plant geography.

Most of these groups cannot be considered primitive in the general phylogenetic sense—as, for example, these nine of the 14 families: the Labiatae, Papilionatae, Mimosoideae, Restionaceae, Centrolepidaceae, Apocynaceae, Myrtaceae, Goodeniaceae, and the subfamily *Caricoideae* of the family Cyperaceae. This would mean that the angiosperms which have developed in Australia since the Upper Cretaceous period cannot be traced back to the very earliest groups of angiosperms. These ancient groups must have developed in much earlier times than the Upper Cretaceous. It is not likely that the nine families have spread from Australia to other parts of the world after Australia's geographic isolation began and that the original primitive species have been conserved in Australia ever since that time. On the contrary, it is much more probable that the primitive ancestral types also existed in other parts of the world even before the Upper Cretaceous period and that they have died out there since that time, just as most of the Marsupialia and the Monotremata have died out in parts of the world outside of Australia. Finally, it should be remembered that it is also possible that the Australian angiosperms of today might have had ancestors originating in other continents before the beginning of Australia's geographic isolation.

It is likely, too, that many of the families of the Australian plants have migrated into Australia in times later than the Upper Cretaceous period, especially those families found now in northern, tropical Queensland.

All of this would mean that parent types of most of the derived families of Angiospermae were already in existence before the Upper Cretaceous period, and that the development of the main branches of the Angiospermae took place in even earlier times. Fossil discoveries lead us to suppose that a strong and rapid development of angiosperms has taken place since the Upper Cretaceous period. Investigations of the



Australian flora do not confirm this impression, however. Rather, they support the supposition that, in most of its essentials, the development of flowering plants goes back to even earlier times—to the period of Lower Cretaceous formations, possibly even as far back as the Jurassic period. Unfortunately there are not many fossil evidences of angiosperms preserved from Jurassic times, and very few of these can be identified with certainty. When the Cenozoic era began, the chief development of the angiosperms must already have been finished. Particularly primitive types might have been preserved until then, of course, but there is no definite fossil evidence as yet of this possibility.<sup>2</sup>

#### COMPARISON OF AUSTRALIA WITH NEW ZEALAND

In this connection it might be significant to draw a parallel by investigating a land area near Australia and which has been isolated from other continents for even a longer time than Australia. Such a territory is New Zealand. No fossil mammals were found there, while, as we know, primitive mammals had entered Australia from southern Asia. In the event that some of these mammals originated in Australia itself—a rather untenable supposition—they must have wandered out of Australia over land bridges toward the north, eventually to reach Europe and North America. In New Zealand, on the other hand, only a small rat has been found to represent the mammals, and this rat was probably imported by man

<sup>2</sup>Erdtman in 1948 published reports in *Grana Palynologica*, that pollen had been found in the black lias formations of southern Sweden. The pollen appears similar to that of *Eucommia* species (*Eucommia* is a genus in China, closely related to the Ulmaceae) and it is not likely to have been derived from Gymnospermae. Inasmuch as the black lias of Sweden is a Lower Jurassic formation, these pollen finds may offer some evidence of the early development of the angiosperms.

in very recent times. The islands of New Zealand have never been connected with land areas inhabited by mammals, and until now no fossil relics of mammals have been found there; it is very unlikely, therefore, that mammals did live in New Zealand at one time but have died out there since.

Now, if New Zealand has never been connected with land areas populated by mammals, where did its flora come from? And does this flora show still more primitive features than does that of Australia?

Diels (1897) has entered into a full discussion of these questions in his work on the *Vegetationsbiologie von Neuseeland*. He assumes that New Zealand has not been submerged since the middle of the Mesozoic era. According to Hutton (cited by Diels, 1897), New Zealand was connected with an Antarctic continent which existed during the Lower Cretaceous period, toward the end of the Mesozoic era. Diels thinks it is probable that, even during the later Triassic period in early Mesozoic time, the Austral circumpolar lands were closely related to each other, so that there was a genetical connection among the mountain floras of Tasmania, southern Australia, the southernmost part of South America, and an Antarctic continent which probably was more temperate in its climate in those early times than it is now. This interrelationship of floras would find its parallel in the Arctic, Alpine, and Altaic floras of the northern hemisphere.

In his paper, Diels cites evidence to support this supposition of the connection of the Antarctic and Austral land masses. In those times the Antarctic continent must have been much larger than it is today, free from ice in its northern parts, and certainly warmer during the Triassic period. In addition to Diel's evidence, we can find further testimony in comparative zoology and in plant geography. Fossil relics of marsupial groups now limited to Australia—species of the

Abderitidae, and of the Sparassodontidae, which are related to the Dasyuridae—have been discovered in Eocene deposits in Patagonia; and Zittel (1895) concluded that "it is an undeniable paleontologic fact that in those times both regions were in mutual exchange or at least drew from the same sources." But only the western isle of the former Australian archipelago (the West Australia of today) participated in this exchange. The eastern islands, particularly New Zealand, did not—because they were not connected either with western Australia or with Patagonia. The most primitive species of marsupials—species of *Myrmecobius* and *Peragalea*—are endemic to West Australia, and it is a very significant fact that there is no fossil evidence to prove that marsupials existed in eastern Australia at any time before the late Cenozoic era, that is to say, before the central Australian sea had retreated (Zittel, 1895: 294). All this is evidence that there must have been connecting land links between Patagonia and western Australia.

We find a very interesting parallel in the distribution of two sections of the genus *Discaria* of the family Rhamnaceae. The section *Notophaena* (Miers) Suessenguth, in its present range, connects Chile and New Zealand. The section *Eudiscaria* Stapf appears in the Argentine countries (that is, in the countries east of Chile), and in Tasmania, Victoria, and New South Wales. This distribution can be explained only by assuming two land bridges leading through an Antarctic continent—one connecting Chile and New Zealand, in a strip slightly arched towards the south; another, farther south than the first, leading from eastern Patagonia through the Antarctic continent to Tasmania and southeast Australia.

It is my opinion that all sketches of these hypothetical land bridges which have been published are not quite correct, for it is impossible—for phylogenetical as well as pale-

ographical reasons—that the connection from Chile to east Australia could have been formed in a straight line. On the contrary, this line passed farther south through an Antarctic continent, which at that time was overgrown with plants.

According to Hutton and Wallace (cited by Diels, 1897), a Melanesian continent connecting New Caledonia, Lord Howe Island, Norfolk Island, and New Zealand, and reaching as far north as the present north Queensland, might well have existed in the Eocene epoch. There was no connection, however, between this continent and western Australia. In Miocene times west Australia and east Australia were connected, but the west Australian species never reached the tropics, and, therefore, did not get to New Zealand.

From these few considerations we learn that the situation in New Zealand is quite different from that in Australia. New Zealand was closely related to the Antarctic continent and to a Melanesian continent, but we cannot expect to find there the primitive species of the Australian continent. The different character of the flora of New Zealand is proof of this expectation. In their *Manual of the New Zealand Flora*, Cheeseman and Oliver (1925) list 1,591 species of vascular plants, with 1,415 phanerogams and 156 vascular cryptogams, among all of which are 1,143 endemic species—72.8 per cent—and 24 endemic genera. While Mueller's catalogue counts 592 species of Proteaceae in Australia, only two can be listed for New Zealand. The large Australian genera of *Eucalyptus* and *Acacia* are completely missing in New Zealand. The floristic connection of New Zealand with Australia is formed by certain of the Myrtaceae (the genus *Metrosideros*) and by the family Epacridaceae. According to Grisebach (1872: II, 633) these are the New Zealand families or groups which are represented by the most species:

PLANT GROUP	NUMBER OF SPECIES	PERCENTAGE OF VASCULAR PLANTS REPRESENTED BY GROUP
Compositae . . . . .	221	14.1
Ferns . . . . .	138	8.8
Cyperaceae . . . . .	119	7.6
Scrophulariaceae . . . . .	113	7.2
Gramineae . . . . .	113	7.2
Umbelliferae . . . . .	62	3.9
Orchidaceae . . . . .	57	3.6
Ranunculaceae . . . . .	50	3.2
Rubiaceae . . . . .	47	3.0
Epacridaceae . . . . .	31	2.0
Onagraceae . . . . .	31	2.0
Leguminosae . . . . .	26	1.7
Juncaceae . . . . .	25	1.6
Boraginaceae . . . . .	25	1.6

The differences between the figures for New Zealand and those for Australia are very striking: Leguminosae, ranking first in Australia, is not among even the first 10 of the families of New Zealand, and neither is Myrtaceae (in second place in Australia), Proteaceae (in third place), or Euphorbiaceae (in eighth place). The Compositae, however, have achieved first place in the New Zealand flora (they are in fourth place in Australia), and—the ferns being left out of consideration—the Scrophulariaceae, the Umbelliferae, the Rubiaceae, and the Ranunculaceae have entered into the list of families with the most species. The Labiatae, in contrast, are not to be found at all in New Zealand; they did not reach these islands from Malaysia and Australia.

Of the 1,591 plant species found in New Zealand, 428 species are not endemic. Among these, 366 are related to the Australian flora, and 108 are related to that of South America.

The genera with the greatest number of species in New Zealand are these: *Veronica*, 84 species; *Carex*, 54; *Celmisia*, 43; *Coprosma*, 40; *Ranunculus*, 38; *Olearia*, 35; *Senecio*, 30; *Epilobium*, 28; *Poa*, 25; *Myosotis*, 23; and *Hymenophyllum*, 20.

It cannot be said, however, that New Zealand's flora is more primitive or has more primitive species than does the flora of Australia, even though its isolation from Malay-

sia and New Guinea apparently occurred earlier than did that of Australia. The great number of endemics in New Zealand's flora, then, can be attributed not to the conservation of primitive species, but rather to the formation of new ones.

Because of its temporary connection with Australia, Melanesia, and the Antarctic continent, New Zealand cannot give us any assistance in solving the problem of the origin of the larger and older Australian flora, so important in any estimation of the age of the angiosperms. The geologic and biologic records left on New Zealand are quite different from those of Australia, and they can not be traced very far back into geologic time.

#### ORIGIN OF NEW TYPES IN AUSTRALIA

How, then, can we explain the appearance of new types in Australia? Perhaps the following supposition may be the simplest one.

Let us assume that during the Upper Cretaceous period, or possibly during the Middle Cretaceous period, but in any case a short time before Australia's geographic isolation began, there existed the plant types A, B, C, D . . . in Malaysia as well as in Australia. Since that time, the Malaysian types have evolved into types A<sup>1</sup>, B<sup>1</sup>, C<sup>1</sup>, D<sup>1</sup> . . . that is, into new and different species or genera. The Australian types, however, have developed into types A<sup>2</sup>, B<sup>2</sup>, C<sup>2</sup>, D<sup>2</sup> . . . into different species or genera from both their parent types, A, B, C, D . . . and the collateral types A<sup>1</sup>, B<sup>1</sup>, C<sup>1</sup>, D<sup>1</sup> . . . developing in Malaysia. It is conceivable that the endemic plants in Australia have evolved in this manner.

Of course it is also possible that this development of endemics could have taken place in later times, without it being necessary for us to conclude that all species of the parent series A, B, C, D . . . must have been distributed throughout Malaysia and



Australia during the Upper Cretaceous period. Many of them may have migrated to Australia in later times, after the separation, and may have evolved there into types A<sup>2</sup>, B<sup>2</sup>, C<sup>2</sup>, D<sup>2</sup>. . . . But if this is true of some plants, it is not likely to be true of the Leguminosae: It is probable that the primitive species of the Mimosoideae, the Papilionateae, and of some of the *other* families listed above (p. 295) immigrated into Australia a long time ago and have survived there unchanged, remaining generally identical with their ancestors of the Upper Cretaceous period, wherever these ancestors may have grown.

For some of the other plant groups, it is possible that their species A<sup>2</sup>, B<sup>2</sup>, C<sup>2</sup>, D<sup>2</sup>. . . may have risen in different epochs. A<sup>1</sup>, B<sup>1</sup>, C<sup>1</sup>, D<sup>1</sup>. . . in Malaysia, and A<sup>2</sup>, B<sup>2</sup>, C<sup>2</sup>, D<sup>2</sup>. . . in Australia, continued to live, while their common ancestors A, B, C, D. . . died out in both territories. Or, if we assume that A<sup>1</sup> = A, B<sup>1</sup> = B, C<sup>1</sup> = C, and so on, or if we take A<sup>2</sup> = A, B<sup>2</sup> = B, C<sup>2</sup> = C, and so on, we might deal, then, with only two lines of development instead of three, and only one of them need have changed—either the one in Australia, since the beginning of its isolation, or the line in Malaysia, since Australia's separation. In other words, the local ancestors of the line A, B, C, D. . . might have died out in one territory and might have been preserved in the other for a very long time. Yet this is not very probable a chance inasmuch as most species of living things—except for the mussels—generally have not been conserved unchanged over long periods of geologic time.

In my opinion this line of approach is the most natural way of explaining the problem. It does not relegate the appearance of all the endemic families of the Australian angiosperms to the apocryphal darkness of antiquity, and yet it does help us to understand the rise of the many endemics in Australia. If we do not insist that all of

these developments took place at almost the same time (in the Upper Cretaceous period) and if we agree that the possibility of subsequent immigrations into Australia must also be taken into account, then we would do well to remember that in their manner of distribution angiosperms and mammals differ markedly in at least this major point: Flowering plants are much more able to cross the sea—if only by means of driftwood—than are mammals. This would seem to be an assertion that could hardly be contested. And yet it is a strange fact that greater numbers of primitive plant types have not been preserved. They became extinct, while the primitive types of animals—the Marsupialia and Monotremata—continued to live. These animals link the mammals with the reptiles, but even at the present time no plants are known in Australia which link the angiosperms with the gymnosperms. The botanical systematist will regret this fact, if only because such proof of primitiveness would be a much more scientific, and therefore a more reliable, basis for the taxonomic system.

My impression of the rise of Australian endemics has been described with reference to its relationship to Malaysia, both because the endemics of this area are more closely related to those of Australia and because of Australia's former connection with New Guinea (see Behrmann, 1937). Perhaps these conclusions will seem quite natural to most readers; nevertheless, I think it would be useful to develop further conclusions based on certain concrete suppositions.

As has been known for a long time, most of the species of the plant families characteristic of Australia grow in the southwestern maritime areas (Hooker, 1860). Fewer species are found toward the north. According to his catalogue, Hooker counted 3,600 species in the southwestern territory, known in his day as Swan River and King George Sound, but only 3,000 from the eastern area,

and only 2,200 from tropical Australia, where the endemic species are fewest in number. Now what is the reason for this distribution? Is it because Malaysia has exerted less of an influence upon these southwestern districts because they are so distant, and because they are separated from the interior—and therefore from the northern shores and Malaysia—by vast deserts? Is this pronounced isolation the reason why more endemic species have developed and have been preserved in the southern periphery of Australia than in its other parts? Or is there a more general rule, as yet unexplained, that endemics are developed more generously in southern lands?

If we compare South Africa with Australia, we can count an enormous number of endemics in Cape Colony; and if we compare the most southern parts of South America—Patagonia and Chile—with Australia, we can find there, too, a great number of endemic species—1,200 of 1,600 species, according to Grisebach's early evaluation in his *Die Vegetation der Erde* (1872: II, 498).

It is not possible to indicate a preponderance of endemics in the most southern part of India, at least on the basis of the figures reported by Hooker and Thomson in their *Introduction to the Flora Indica* (1855). Newer statistics concerning Indian endemics apparently are not yet published.

In Europe, however, the majority of endemics is found in the southern areas, particularly in the Balkans and in Crete (Turrill, 1929). In this connection, Newbigin (1936) has made these statements about mammals: "It has been made abundantly clear that the great migratory movements have been from the wide land masses of the northern hemisphere towards the narrower and discontinuous southern ones, and that extinction of early stocks has been most marked in the Holarctic region, while the survival of members of these is especially characteristic of some of the southern lands. . . . The past and present distribution of the higher plants con-

firms the conclusions derived from the study of mammals. Sometimes the correspondence is curiously exact." Unfortunately, Newbigin does not give his proofs of these lapidary sentences, particularly for the plants. Let us, therefore, find our own proofs in some examples from the pertinent literature.

A good many of the flowering plants, as, for example, the families of the Papaveraceae and the Geraniaceae, have migrated along the ridges of the Andes, from both North America and Central America, far into South America (Vester, 1940: 162, fig. 78). The genus *Ribes*, which also migrated in this manner, has been cited for this fact by Newbigin (1936). The same evidence of migration appears to be provided for some of the Primulaceae, with *Primula farinosa* in the Holarctic region and in Andean Patagonia (Vester, 1940: 154, fig. 40); for the Betulaceae (*ibid.*, 163, fig. 80); for the Empetraceae (*ibid.*, 163, fig. 81); for the Orobanchaceae (*ibid.*, 164, fig. 86); and for the Juglandaceae (*ibid.*, 176, fig. 153).

Fossil discoveries give further evidence that, to a great extent, some of the plant groups were forced out of northern areas into southern not only by diluvial glaciers, which, coming from the north, destroyed the Cenozoic flora of central Europe and of central North America, but also by hitherto unknown factors which were effective much farther southward. The Magnoliaceae, for instance, at one time must have grown over vast parts of the Holarctic region, but today they are limited to South and Central America, eastern and southeastern North America, the West Indies, southwestern Asia, Malaysia, eastern Australia, and New Zealand (Vester, 1940: 188, fig. 262). The Juglandaceae, too, have disappeared from large areas of northwestern North America, from Europe (except for the Balkans), and from central Asia (except for the Caucasus), while in the more southern regions they continue to survive. Further examples are to be found in the fam-

ily Ebenaceae, according to Fernald (*in* Vester, 1940: 174), and in the tribe Cycadeae and the genera *Podocarpus* and *Araucaria*, according to Studt (1926).

It is doubtful whether any instances can be found to prove a considerable migration of a plant flora in the opposite direction, that is, from south to north. It is true, of course, that a number of plants, reported by Suesseinguth (1942), have worked their way northward from the South American Andes, reaching as far north as Costa Rica and Mexico. However, these migrations have taken place only since the Miocene elevation of the Cordilleras in Central America, and they are rather insignificant compared with the major southward migrations.

There is evidence, however, that north-eastern Africa has been reached from a north-eastern direction by species of plants from India and western Asia.

Although it might be expected that the Mediterranean floral elements might have arrived in central Europe from the south, following the retreating glaciers as they withdrew to the north, I do not think this argument is tenable, inasmuch as it is quite possible that representatives of the Mediterranean flora might have found refuges in the climatically favorable parts of central Europe during the glacial advances. It is much more likely that the North American plants of Cenozoic time were forced southward by the glaciers, and then, after the glaciers had retreated, were permitted to return north, to recover vast territories of their former areas of distribution. Nonetheless, these instances of northward migration are abundantly surpassed by the notable removal to the south of plants in Australia, the Andes, Patagonia, Cape Colony, and the Balkans, in all of which real displacements to the south have been demonstrated. During the cold periods of the glacial advances, all of the hydro-megatherms and megatherms should have been concentrated towards the tropics from the Arctic

and Antarctic regions, and it is not to be denied that a large part of the "small belt-like areas" of many families in the whole tropic range may thus have been established in their present ranges (Vester, 1940: 166 *et seq.*, figs. 93-113). Nevertheless, it seems as if in Australia, the Andes, Africa, and Europe other factors had contributed to force a great number of species of plants from the north to the south, and in those areas in the southern hemisphere this displacement carried the plants even farther south than the Tropic of Capricorn.

This phenomenon of displacement from north to south does not need the supposition of some mystical power to explain it. In Africa, for example, a northward counter-displacement of the ancient flora of the northern and middle part of the continent could not happen because it was blocked in that direction by the broad Tethys sea of the early Tertiary period (Eocene time, and so on) or by the deserts that are its relics. Australia, to give another example, in post-Tertiary time could not receive plants from any direction but from the north, because it was only there that Australia was connected, if only temporarily, by land bridges with large masses of land, while in the south the Antarctic continent at a later period was too cold and too far distant to permit of plant migration. In the Andes plant distribution is not as easily explained. In the Balkans the lowering of temperatures in the north by the glaciers may have played a part in the southward displacement of the plant life, so that numerous types of plants died out in the north which continued to live in the south. It would be of great interest to investigate the degree of displacement in still other parts of the world.

Many other objections might be raised to dispute this claim of the southward displacement of plants. The major point of dispute is whether or not this southward displacement of certain systematic groups—such as,

for example, the Magnoliaceae, which are said to be analogous in this respect to many animal groups—can be attributed only to the lowering of temperatures in the northern regions during the time of glaciation.

#### CONCLUSION

These investigations have offered statistical evidence that the phylogenetically older types of about 10 large taxonomic groups of the higher plants are found, either exclusively or in their great majority, in Australia. By analyzing the floras of the lands near Australia today, and by drawing analogies from the floras of the southern parts of all of the other continents, it can be concluded that the ancestors of the Australian plants must have existed in Australia during the times of the Upper Cretaceous period. This can be the only conclusion because it would be impossible for the Australian flora to form one vast atavism, if only because atavisms are rare, when they are encountered at all, and usually play no part in the formation of species.

It should be stressed that in order to reach this conclusion no contrived assumptions were made regarding the primitiveness of the characteristics of the Australian plants: Concepts and judgments of primitiveness were based entirely upon the well-established criteria of the older taxonomic systems (the *Natürliche Pflanzenfamilien* of Engler and Prantl, for example) and upon the general discussions of phylogenetically important characteristics given by Wettstein in his handbook of systematic botany (1935) and by myself (Suessenguth, 1938), without dependence upon rules or criteria established particularly for the Australian flora. The special questions of the phylogenetic age of Australian families put in this paper, and the answers proposed to them, have not been presented before, to my knowledge.

The data obtained in these investigations would suggest that natural immigrations of plants into Australia, after the beginning of

its isolation from Malaysia, were not very likely—or at least were not very plentiful—the enormous degree of endemism which Australia now exhibits being evidence against any considerable change in later times.

It cannot be established with certainty whether or not the plants of the primitive genera of the 10 major Australian families are not only endemic by preservation but are also plants which have originated in Australia and which have existed there since their beginning to become the ancestors from which the families have spread throughout the world. In the majority of cases I do not think it likely that these plants have been disseminated from an Australian center inasmuch as paleontological evidence concerning animals shows that many animals which at one time were widely distributed have been preserved alive in Australia while they have become extinct in other regions. Obviously, what has happened to animals could also have happened to plants.

We can conclude, however, from the indirect evidence presented by the Australian flora that the development of primitive families of the angiosperms must have taken place during the Middle and Lower Cretaceous period or, possibly even earlier, during the Jurassic period. But this conclusion, while it is supported by the endemic nature of the Australian flora—which, of course, was isolated when the connection of Australia with Malaysia was ended in the Upper Cretaceous period—has yet to be confirmed by the discovery of fossil evidences of angiosperms in formations of those Middle Mesozoic times.

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# The Osteology and Relationships of the Echelid Eel, *Kaupichthys diodontus*<sup>1</sup>

WILLIAM A. GOSLINE<sup>2</sup>

## INTRODUCTION

THE MAIN FUNCTIONS of the present paper are to demonstrate that two very different families of eels have hitherto been included under the "Echelidae" and to allocate these families to their proper positions in the order Anguilliformes (or Apodes). In order to establish these points, the osteology of *Kaupichthys diodontus* Schultz is dealt with in some detail.

On September 7, 1949, an unripe female of this species, 155 mm. long, was taken by Strasburg, Welsh, and the author in a poison station in shallow water off the aquarium at Waikiki, Oahu, Territory of Hawaii. The species (and genus) was originally described by Schultz (1943: 50, pl. 6 and text fig. 5i) from Tau and Rose Islands in the Samoan group. It is hitherto unrecorded from Hawaii. The specimen at hand differs from Schultz's description (and from a Bikini specimen dealt with below) as follows: the teeth are blunter than indicated in his diagnosis and figure (5i); the two rows of vomerine teeth are not so widely separated, nor do they extend farther posteriorly than the maxillary rows; and finally, the maxillary teeth are quite distinctly set apart from the premaxillary and vomerine groups. Whether the Hawaiian form merits specific or subspecific distinction, or whether the above-mentioned differences are merely individual or size variations, I do not have sufficient material to decide.

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In identifying the Waikiki specimen I became doubtful as to its relationship with the other Hawaiian genus—*Muraenichthys*—which has always been placed in the same family with it (Schultz, 1943: 49; Schultz and Woods, 1949: 170). A specimen of *Kaupichthys diodontus* from Bikini, one of the duplicates very kindly sent me by Dr. Schultz, permitted an osteological investigation of that species. From this examination it is very apparent that *Kaupichthys* and *Muraenichthys* do not belong in the same family; in fact they belong on opposite sides of the major division of the eels as classified by Regan (1912) and Trewavas (1932). An account of the osteology of *Kaupichthys*, based on the 100 mm. specimen from Bikini, follows. The specimen was stained in alizarin and the head dissected; the remainder of the specimen was cleared in potassium hydroxide.

## OSTEOLOGY

The lateral line canals of the body and head are enclosed in a series of small bony ossicles except where they penetrate the skull bones. That of the body gives rise to only two pores leading to the exterior; these are both forward of the pectoral (Fig. 1). In the head region the sensory canal system is of rather normal eel pattern (Trewavas, 1932, pl. 4b and text fig. 3A), though the number of pores leading to the surface of the head is somewhat reduced. A longitudinal canal (ll) connects the lateral line of the body with that of the head system. As is usual in eels, a transverse canal (tc) run-



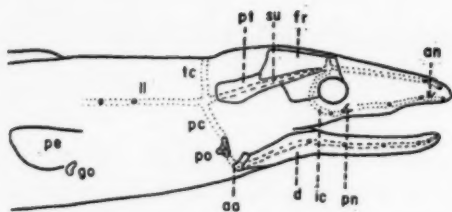


FIG. 1. Outline of head region of *Kaupichthys diodontus* indicating the course of the lateral line canals. Areas in which the canals pass through flesh are shown as dotted lines; areas in which canals pass through bone are shown in dashed lines with the outlines of the bones drawn in. Pores opening to the exterior from the canal system are shown as circles. aa, Articular-angular; an, anterior nostril; d, dentary; fr, frontal; go, gill opening; ic, infraorbital canal; ll, lateral line; pc, preopercular canal; pe, pectoral fin; pn, posterior nostril; po, preopercle; pt, pterotic; su, supraorbital canal; tc, transverse postcranial canal.

ning up and across the nape just behind the skull connects the longitudinal canals of the two sides of the body; it gives rise to a series of pit organs externally but to no pores. The preopercular canal (pc) exits ventrally from the longitudinal canal opposite the junction of the latter with the one crossing the nape and proceeds anteroventrally through the preopercle and into the articular-angular and dentary in a normal manner. The longitudinal canal itself passes forward into the head as the supraorbital canal (su), which runs the entire length of the pterotic and through a short section of the frontal; from here it passes forward in a tube—all that is left of the nasal—to the tip of the snout. In addition, a short branch runs mesially in the frontal, but does not meet its fellow from the other side, nor does it give rise to a pore to the exterior. The infraorbital canal (ic) emerges from the supraorbital system in the frontal, runs laterally and then downward behind the eye and finally forward in the upper lip to the tip of the snout; in the lip it runs mesial to the posterior nostril and below the anterior nostril. The pores open-

ing to the exterior from the lateral line system are shown in Figure 1.

The suspensorium of *Kaupichthys* (Fig. 2) is vertically suspended, i.e., the articulation between the quadrate (q) and the articular-angular (aa) lies but slightly behind the center of the hyomandibular (h). The palatopterygoid (pp) is laminar and well developed for eels, but appears to be unattached, except by a ligament, either before or behind. The maxillary (m) articulates with the combined premaxillary, ethmoid, and vomer (ev) near the tip of the snout. The opercular apparatus is reduced. The preopercle (po), which remains chiefly as a tube for the lateral line canal, overlies the broadly wedge-shaped interopercle (io). The subopercle (sr) completely encircles the opercle (op) below. The top half of the normal fish opercle is gone, only the lower half remaining.

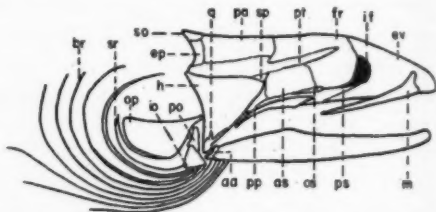


FIG. 2. Head skeleton with suspensorium, jaws, opercular bones, and branchiostegal rays. Teeth are omitted, and all the branchiostegal rays are not shown: as, Alisphenoid; br, branchiostegal ray; ep, epiotic; ev, premaxillary-ethmo-vomer; fr, frontal; h, hyomandibular; if, interorbital foramen; io, interopercle; m, maxillary; op, opercle; os, orbitosphenoid; pa, parietal; po, preopercle; pp, palatopterygoid; ps, parasphenoid; pt, pterotic; q, quadrate; so, supraoccipital; sp, sphenotic; sr, subopercle.

In the cranium (Fig. 3a-d) the premaxillaries are ankylosed to the ethmo-vomer. The orbitosphenoid (or) is a long, slender bone wedged between the parasphenoid (ps) below and the alisphenoid (al) and frontal above. The enlarged otic bulla (ob) is composed ventrally of the basioccipital (bo) and the prootic (pr); it contains a large sagitta

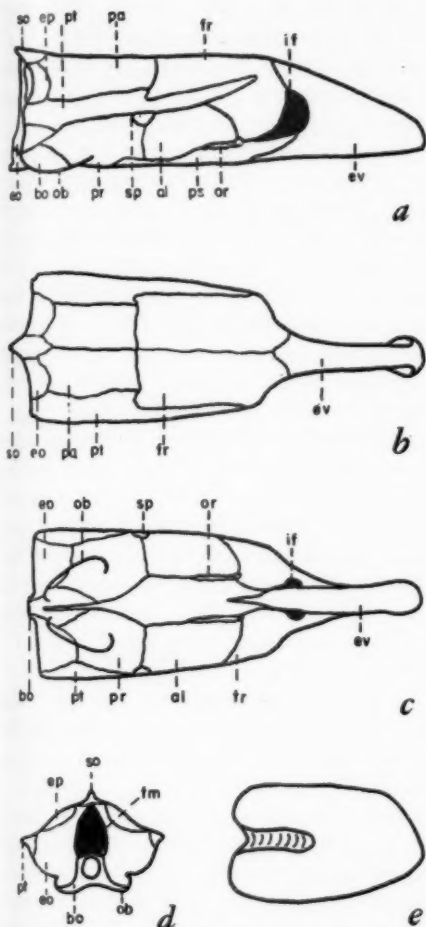


FIG. 3. *a*, Cranium from the side; *b*, from above; *c*, from below (teeth omitted); *d*, from behind; *e*, sagitta. al, Alisphenoid; bo, basioccipital; eo, exoccipital; ep, epiotic; ev, premaxillary-ethmovermer; fm, foramen magnum; fr, frontal; if, interorbital foramen; ob, otic bulla; or, orbitosphenoid; pa, parietal; pr, prootic; ps, parasphenoid; pt, pterotic; so, supraoccipital; sp, sphenotic.

(see Fig. 3*e* this paper and Frost, 1926: 99). On the dorsal surface of the skull the frontals are completely divided by suture; the parietals (pa) are rather large for eels; the pterotics are elongate. On the posterior face of the skull the foramen magnum (fm) is large

and the socket for the articulation of the vertebral column relatively small for eels. The first vertebra is not fused to the skull.

The branchial apparatus (Figs. 4 and 5) is of normal eel type, without specialized features. There are 15 branchiostegal rays (br) on each side; those of the two sides of the head do not overlap on the midventral line and rather closely encircle the opercular bones behind. The upper pharyngeals (up) articulate with the upper ends of the third and fourth branchial arches. The fourth arch closely adjoins the lower pharyngeals (lp) below. Both upper and lower pharyngeals

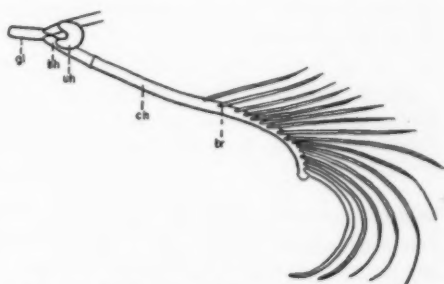


FIG. 4. Right side of hyoid arch, from below. bh, Basihyal; br, branchiostegal ray; ch, ceratohyal; gl, glossohyal; uh, urohyal.

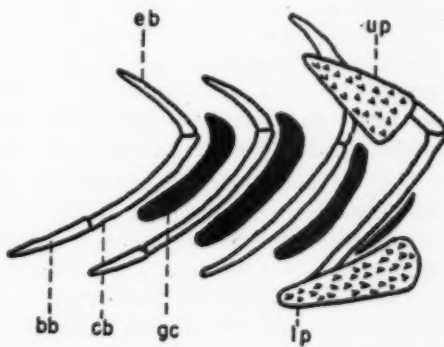


FIG. 5. Median view of right gill arches, somewhat opened out. bb, Basibranchial; cb, ceratobranchial; eb, epibranchial; gc, gill cleft; lp, lower pharyngeal; up, upper pharyngeal.

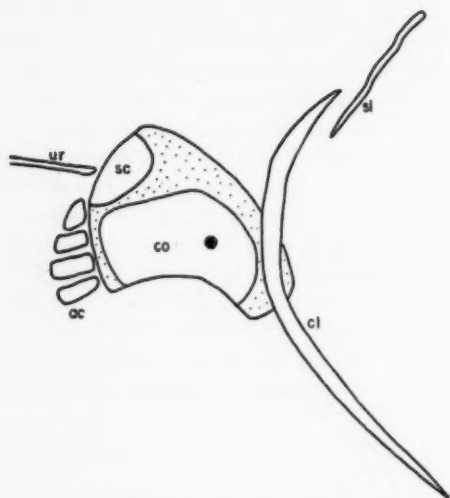


FIG. 6. Lateral view of right side of pectoral girdle. Cartilage stippled. ac, Actinost; cl, cleithrum; co, coracoid; sc, scapula; sl, supracleithrum; ur, upper pectoral ray.

bear conical teeth. The openings between the first four gill arches are wide; that between the fourth and fifth is restricted.

The pectoral girdle of *Kaupichthys* (Fig. 6) is rather well developed for eels. The supracleithrum (sl) lies free in the flesh without articulation above or below. The cleithrum (cl) is a long, curved bone overlying the forward end of the endoskeletal girdle. The coracoid (co) and scapula (sc) are embedded in a cartilaginous plate. There are four actinosts (ac), of which three and a half articulate with the coracoid area.

The vertebrae number approximately 98. Of these, about 20 lie ahead of the anus. However, the numbers of preanal and abdominal vertebrae are not the same, for the coelomic cavity of this fish extends posterior to the anus, as does the portion of the vertebral column without closed haemal arches.

The short centrum (ce) of the first vertebra (Fig. 7a) has a rounded head fitting the socket of the basioccipital. It bears a neural arch (na), which extends backward over the

centrum of the second vertebra. The second vertebra, in addition to the neural arch, has a median ventral projection. The third is similar to the second but bears a well-developed transverse process pointing postero-laterally. The neural arches of the first few vertebrae have crests with two to several dorsal spinules. These small spines drop out behind about the fifth vertebra. Farther back along the vertebral column each neural arch gives rise to a neural spine, these becoming well developed over the middle of the caudal portion of the vertebral column, but diminishing again posteriorly, and dropping out completely over the last nine vertebrae.

Over the whole rear part of the abdominal section of the column the vertebrae develop broad, flat, lateral flanges. These, however, fail to bear ossified ribs. In fact, there appear to be no articulated ribs anywhere in the fish. Nevertheless, there are, in the caudal section, what appear to be long, slender, unarticulated epipleurals and epineurals for each vertebra (not shown in Fig. 7c).

Posteriorly the haemal canal seems to stop at the seventy-eighth vertebra. The haemal spines (Fig. 7c, hs) continue to the ninety-third. The final vertebra (Fig. 7b and d) is extremely elongate. It appears to be made up in part of a rudimentary centrum, with neural and haemal arch, and in part of endoskeletal elements (ee) of several fin rays. These endoskeletal elements form three groups united to the rest of the vertebra by a cartilaginous plate containing a large foramen (fo).

The heart lies just behind the gill arches and immediately before the level of the pectoral girdle.

#### RELATIONSHIPS

The osteology of *Muraenichthys* closely resembles that of the Ophichthyidae (to be dealt with in a forthcoming paper) and differs vastly from that of *Kaupichthys* described above. The frontals of *Muraenich-*

*thys* are fused; the orbitosphenoid is short and rounded; the otic bulla is little developed; the parietals and pterotics are far smaller; the suspensorium is somewhat forwardly inclined; and the branchiostegal rays are long, fine, and numerous. Still other differences between the two genera are to be found in the pectoral girdle and vertebral column.

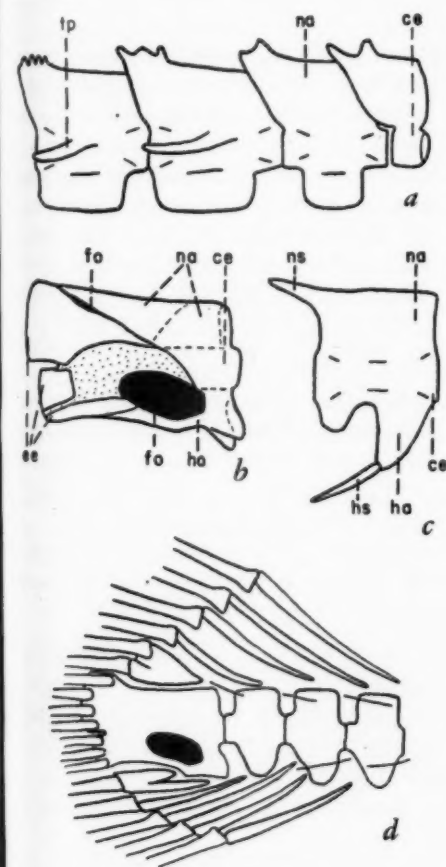


FIG. 7. *a*, First four vertebrae, lateral view of right side; *b*, terminal vertebra (cartilage stippled); *c*, seventy-ninth vertebra; *d*, last four vertebrae plus endoskeletal and bases of exoskeletal elements of fin rays. ce, Centrum; ee, endoskeletal elements of fin rays; fo, foramen; ha, haemal arch; hs, haemal spine; na, neural arch; ns, neural spine; tp, transverse process.

Since both *Muraenichthys* and *Kaupichthys* have always been included in the Echelidae, a question of the allocation of the family name arises. It is obvious from Regan's diagnosis (1912: 380 and 386) of his family Echelidae that he investigated the *Muraenichthys* type of eel. On the other hand, from the descriptions of *Echelus myrus*, the genotype of *Echelus*, given by Richardson (1844: 108), Günther (1870: 50), and Jordan and Davis (1892: 642), it appears that the family name Echelidae belongs with *Kaupichthys*. The *Muraenichthys* type can probably best be placed within the Ophichthyidae, following the suggestion of Myers and Storey (1939: 157), as a subfamily, Myrophinae. However, the final applications of the names Echelidae and Myrophinae (or Myrophidae) must await an osteological examination of *Echelus myrus*, a Mediterranean species unavailable to me.

The family Echelidae in the sense used just above, i.e., limited to the *Kaupichthys* type of eel, shows distinct relationship to the Moringuidae and Heterenchelidae in the paired frontals, and particularly in the enlarged otic bulla. It differs from either of the latter families in possessing relatively high vertical fins and labial posterior nostrils. It resembles the Heterenchelidae but not the Moringuidae in the long, narrow orbitosphenoid, in the laminar palatopterygoid, in having the trunk shorter than the tail, and, apparently, in the movable articulation between the first vertebra and the skull. It resembles the Moringuidae but not the Heterenchelidae in lacking a suture between the ethmoid and the vomer. Thus the relationships of *Kaupichthys*—and provisionally of the Echelidae—are closest with the Heterenchelidae.

The fact that *Kaupichthys* and *Muraenichthys* belong to different families also raises the problem of the family allocation of the remaining genera assigned to the Echelidae *auctorum*. Some, such as *Garmanichthys*, appear to belong with *Kaupichthys*. Others,

for example *Myrophis*, are of the *Muraenichthys* type. The superficial similarity between the two groups makes the problem of properly placing the genera particularly complex. Both have no free tongue, have the posterior nostril on the upper lip, the dorsal and anal confluent around the tip of the tail, and the gill opening consisting of a small hole. Within the Myrophinae the position of the anus and of the origin of the dorsal vary considerably, and the pectoral fin may be present (as in *Myrophis*) or absent (as in *Muraenichthys*); consequently these characters cannot be used to separate the Myrophinae from *Kaupichthys*.

The only superficial distinction that I can find between the groups is the presence in the Myrophinae of a swollen gullet supported by a basket-like arrangement of the numerous, long branchiostegal rays (Parr, 1930: 71), and the absence of these characters in the *Kaupichthys* type of eel. Other distinguishing external characters could probably be found if adequate comparative material were available.

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# The Genesis and Morphology of Hawaiian Ferruginous Laterite Crusts<sup>1</sup>

G. DONALD SHERMAN<sup>2</sup>

MASSIVE FERRUGINOUS SOIL HORIZONS have been discovered in the profiles of certain Hawaiian soils which have morphological characteristics similar to the ferruginous laterite crusts found in other tropical areas. Likewise, the nature of the soil weathering responsible for these ferruginous horizons bears a great resemblance to that described for other ferruginous horizons. However, the ferruginous soil horizons found in the Hawaiian Islands do not have the hardness which is described for ferruginous crusts in India or Indo-China. In spite of the lack of this degree of hardness the author feels that the Hawaiian soils which have a hard ferruginous surface or near-surface horizon are the equivalent of the ferruginous laterite crust of other tropical regions. It is the purpose of this article to describe the genetic and morphological characteristics of the Hawaiian laterite crusts and to show their similarity to other described laterite crusts.

The original description of a laterite was made by Buchanan (1807), who defined it as a ferruginous indurate clay which is brick-like in nature. Pendleton (1946), a firm follower of Buchanan, has defined a laterite as follows: "Illuvial horizon largely iron oxides, slaglike, cellular or pisolitic structure, and of such a degree of hardness that it may be quarried out and used for building construction." Many of the temples in tropical Asia are built of these laterite materials. Du

Preez (1949) has modified Pendleton's definition in that he describes a laterite to be a vesicular, concretionary, cellular, vermicular, slaglike pisolitic or concrete-like mass consisting chiefly of ferric oxides with or without mechanically entangled quartz and minor quantities of alumina and manganese; it is of varying hardness but it is usually easily shattered when struck a sharp blow with a hammer. Du Preez's definition differs from Pendleton's in that it does not require a degree of hardness to meet the requirements of a material suitable for building construction. Botelho da Costa and Lobo Azevedo (1949) have objected to a definition of a laterite which requires the presence of a concretionary ferruginous layer. In general, Du Preez's definition has considerable acceptance.

Sherman (1949) has pointed out that the laterite crust will be the end product of tropical soil weathering under an alternating wet and dry season. He has suggested that under continuous moist soil conditions the ultimate end product of soil weathering in the tropics will probably be a soil rich in alumina. The ferruginous layer which occurs at or near the surface is called a laterite crust in that it is usually a hard sterile soil area. The ferruginous layer may be found below the surface which may have resulted from erosion or by formation over the water table in coarse-textured soils. The ferruginous layer which develops in the fine-textured soils materials forms below the surface and is later exposed by erosion as sterile hard surface soil.

## HAWAIIAN LATERITE CRUSTS

Hawaiian soils having hard sterile surfaces have been described by Sherman *et al.*

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<sup>2</sup>Chairman, Department of Soils and Agricultural Chemistry, University of Hawaii Agricultural Experiment Station.

(1949). These soils have a surface horizon which is a compacted or vesicular slaglike mass having a very high apparent specific gravity. Some of these areas are covered with a sparse dwarfed vegetation while others are practically barren areas in which the surface soil has a glazed surface with the hardness of a pavement. The high apparent specific gravity is due to presence of large quantities of iron and titanium oxides which make up more than 75 per cent of the soil. The hard sterile ferruginous laterite crusts have been found on the southern and western slopes of the island of Kauai; on the western slope of the main mountain range of Molokai; and on the white trachyte cliffs of West Maui. In every case the areas are found on long slopes in which heavy rainfall is received at the higher elevations while the lower elevations remain very dry. The areas of hard crusts are found just below the lower boundary of the canopy forest.

#### MORPHOLOGICAL DESCRIPTIONS OF HAWAIIAN LATERITE CRUSTS

##### *Island of Kauai*

The hard sterile laterite crusts are found on the southern and western slopes of leeward Kauai. These areas are found on the benches or on broad and more level areas of the long ridges which run from the top of the mountains toward the ocean. The hard surface crusts are found in the transition zone between the shrub vegetation on the lower elevations of the slope and the dense canopy forest cover on the wet higher elevations of the slope. The surface horizon of the crusted areas is a very hard compacted purple silt loam having a very high apparent specific gravity. The volume weight of this layer approaches 3.0 in some cases. This horizon is very hard and it is necessary to use a heavy sharp tool to break the layer. The chipped-off fragments crush readily in one's hand to a very fine graphite-like powder. This pow-

dery material contains small pellets of magnetite. About 30 per cent of the particles are of clay size, but even so this material does not exhibit any evidence of stickiness when wet. The thickness of the crust may vary from 4 to 14 inches.

The hard surface layer is underlain by a yellowish-brown to reddish-brown friable silt loam. There is very little evidence of heavy minerals which were responsible for the high apparent specific gravity of the surface horizon. While this soil has the physical properties of a silt loam, mechanical analysis of the soil showed that more than 60 per cent of the soil particles are of clay size. The thickness of the friable layer ranges from 12 to 36 inches.

The friable layer lies over an impervious surface of an unconformity or an impervious soil horizon. In the former case the material is of different geological formation than the material from which the soil was formed. In the latter case it has not been established whether the impervious soil horizon is related to the soil solum or is the surface of a buried soil. Whether or not this plastic subsoil is related to the soil, it has provided an impervious layer which, apparently, is necessary for the formation of ferruginous laterite crust.

The chemical analysis of a typical Kauai ferruginous laterite crust is given in Table 1. The high content of iron and titanium oxides in the hard crusted surface horizon is characteristic of these soils. The iron oxide exists as hematite, and titanium oxide as anatase.<sup>9</sup> Another characteristic of the analysis of this horizon is the low content of volatile matter. The B horizon has an iron oxide content ranging from 70 to 80 per cent. The iron oxide of this horizon exists as goethite and hematite. The titanium oxide content of this layer is markedly lower than is that of the hard surface horizon. The chemical composition

<sup>9</sup>Cooperative studies with Dr. M. L. Jackson, University of Wisconsin.



TABLE I  
THE CHEMICAL COMPOSITION OF A TYPICAL FERRUGINOUS LATERITE PROFILE. THIS PROFILE IS  
LOCATED OFF THE KOKEE ROAD ON KAUAI

HORIZON	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	TiO <sub>2</sub>
<i>inches</i>	<i>per cent</i>	<i>per cent</i>	<i>per cent</i>	<i>per cent</i>
Surface 0-3	10.8	10.7	38.2	19.4
Ferruginous Crust 3-11	3.8	9.9	47.5	25.1
Friable Layer 11-27	5.5	7.6	78.5	7.2
Plastic Clay 27+	22.8	21.7	35.4	3.3

of the impervious horizon is very different from that of the other two horizons. The higher content of both silica and alumina indicates the presence of aluminosilicate clay minerals.

#### *Island of Molokai*

The hard, compacted, ferruginous laterite crusts are found on the westerly slopes of the mountain range. The areas of this soil are found in the zone of the open forest, just below the heavier canopy forest of the wetter, higher elevations. These areas are easy to observe because of their distinct purple color and shiny glazed surfaces. The hard surface layers of these laterite crusts are harder and more compacted than are those found on Kauai. The areas of this soil are limited to a very narrow belt on Molokai, whereas the laterite crusts are found over a much wider area on Kauai. The hard surface crust of these soils is very similar to those found on Kauai. The chief profile difference occurs in the friable layer. The friable layer below the hard surface horizon of the Molokai laterite crusts is very thin, ranging from 4 to 8 inches. In every observed instance the friable layer lies over a solid rock formation.

The physical and chemical compositions of the Molokai laterite crusts are very similar to those of the Kauai laterite crusts. The iron oxide content of the surface ranges from 48 to 65 per cent and the titanium oxide from

20 to 24 per cent. Likewise, the volatile matter ranges from 3.2 to 4.2 per cent. The iron oxide content of the friable layer ranges from 70 to 76 per cent.

#### *West Maui*

The ferruginous laterite crusts of West Maui occur as erosion remnants on the white trachyte cliffs. These areas are easily seen from an airplane. From the highway these areas can be seen as red caps on top of the grayish-white ridges running up the mountain slope. These areas are so badly eroded that in only a few locations does the profile remain intact. In one case the hard surface crust has slid away from its friable layer and the two now exist as separate erosion remnants.

The hard surface horizon is a compacted, reddish silt loam having a high apparent specific gravity but lower than that found for Kauai and Molokai laterite crusts. The surface of these crusts is hard but does not have the shiny glazed surface of the two other areas. The clay content of this horizon is higher, being more than 35 per cent.

The friable layer of these soils has all the characteristics of the Kauai profile. It is very ferruginous and has a clay content exceeding 65 per cent. The thickness of the friable layer has been found to range from 12 to 30 inches.

TABLE 2  
THE CHEMICAL COMPOSITION OF TYPICAL HAWAIIAN FERRUGINOUS LATERITES  
AND SIAM FERRUGINOUS LATERITES\*

LOCATION OF FERRUGINOUS LATERITE	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	TiO <sub>2</sub>	TOTAL
Kauai—Waimea Canyon	<i>per cent</i> 3.9	<i>per cent</i> 5.8	<i>per cent</i> 60.8	<i>per cent</i> 26.0	<i>per cent</i> 96.5
Molokai—Just below forest line	7.8	3.6	60.4	24.0	95.8
Maui—From eroded trachyte cliffs	5.8	12.0	64.8	11.2	93.8
Siam—Ferruginous concretion	11.8	30.0	46.2	1.8	89.8
Siam—Ferruginous lens	15.4	24.8	51.2	2.4	93.8

\*Samples of Siam ferruginous laterites were given to the author by Dr. R. L. Pendleton. The sample analyzed was from a portion of the specimen showing the greatest evidence of iron deposition.

These soils have developed from the trachyte rock on which they are found. Even though these are residual soils, there is a sharp boundary between the unweathered trachyte rock and the soil solum.

The chemical composition of the ferruginous laterite crust from West Maui is given in Table 2, along with the analysis of ferruginous laterite horizons from Kauai and Molokai. Also included in Table 2 are samples of Siam laterites. The difference in the analyses indicates that Siam is not as old as the areas on Molokai and Kauai, or that the difference may be due to the nature of the more acidic parent material. Some of the crusts which occur at inaccessible higher elevations appear to have progressed further in their development than those at the accessible lower elevations.

#### SOIL WEATHERING CYCLE INVOLVED IN FERRUGINOUS LATERITE CRUST FORMATION

The ferruginous laterite crusts have developed in Hawaii under certain definite weathering conditions. It has been pointed out that the ferruginous laterite crusts have formed on long slopes which have a heavy annual rainfall region at the higher elevations and a low annual rainfall at the lower elevations. Certain other characteristics always appear to be necessary for the crust

formation. The impervious layer, whether an unconformity or impervious clay layer, is always found below the friable horizon. If one examines the lower portion of the friable layer, indications of the lateral movement of water will be observed. This has been substantiated by the very wet condition found in this layer at a period of several days after heavy rainfalls at the higher elevations. The lateral movement of water through the friable layer has been demonstrated by the seepage of water into wells dug in this type of a soil. The hard crust surfaces are formed in areas of the slope which are either a bench or the more level areas of the slope. The last condition, a very important one, is that the crusts are formed in a climatic region which has a very dry season alternating with a wet season. The greatest development occurs in the regions where the wet and dry seasons are of about the same duration. A typical case would be 4 months with less than 2½ inches of rainfall and 3 months having more than 4 inches of rainfall. Some of the dry months may have less than an inch of rainfall; thus, the vegetation of the area will be the type which falls between the shrub vegetation of the drier areas and the tropical canopy forest of the wetter areas.

The two factors which appear to be most responsible for the development of the

crusted surface horizons are the lateral movement of water through the friable layer and the alternating wet and dry season. The water moving laterally through the friable layer would contain dissolved ions from the weathering of the soils under a heavy rainfall condition where the soil solum is continuously moist. Sherman (1949) has shown that in these soils iron oxides are being reduced and are being leached away in the percolating water. He also pointed out that titanium content of these wet soils is low as compared to other Hawaiian soils. Thus it is possible for the percolating waters of these soils to contain iron in a reduced form and titanium as a hydrated titanium oxide or in an acid form. The former has been identified by Doelter (1913) in laterite soils, and the latter is possibly due to the very acid condition of the soils of the very wet locations. The waters would also contain a small amount of dissolved silica. The greater portion of the silica is removed during the earlier stages of soil weathering and when the internal drainage of the soil profile was good. As the soil matured, the internal drainage became poor due to the development of impervious clay layers. With the development of the poor internal drainage more of the percolating water will move down the slope laterally and less will percolate through the soil and its weathered parent material. When the lateral movement of percolating water reaches areas having an alternating wet and dry season, conditions become favorable for the capillary rise of the percolating waters during the dry season. The capillary rise of the percolating waters to the surface is greatly enhanced by the benches or level areas of the slopes. A similar case of enrichment of soils of lower elevations by lateral movement of percolating waters has been proposed by Green (1947).

The dissolved iron and titanium are brought to the surface in the capillary water. The iron is stabilized by its oxidation to the

ferric form. During the dry season the iron oxide, which probably exists as goethite, and the hydrated titanium oxides are dehydrated to form the minerals hematite and anatase, respectively. The dissolved silica in the percolating waters would probably rise to the very surface before dehydration. The data in Table 1 would support this hypothesis. The lack of an appreciable amount of titanium oxide in the friable layer would suggest that the titanium must move as a colloidal hydrated titanium oxide. Fujimoto *et al.* (1949) have reported the titanium oxide content of 45 per cent in the colloidal fraction of the transitional zone between the friable layer and the laterite crust horizon. The low content of volatile matter, which would include water of hydration, suggests that both titanium and iron oxides are stabilized by dehydration. This would account for the presence of the two secondary minerals hematite and anatase in the surface soil. The ilmenite content of these soil horizons is extremely low and would rule out the possibility of residual concentration. Furthermore, if ilmenite did not decompose under tropical soil weathering, titanium should be concentrated in greater quantities in the surface horizon of the soils developed in the regions of heavy rainfall as well as where it is found in the area having the hard surface crusts. The chemical analyses of these soils do not reveal a concentration of titanium. In Figures 1 and 2 are given the graphical representation of the manner in which the ferruginous laterite crusts have become the zone of accumulation of iron and titanium oxides.

The ferruginous laterite crust is considered to be the senile stage of tropical soil weathering under a climate having alternating wet and dry seasons. Thus as the crust area becomes denuded of vegetation it will remain a stabilized land form until removed by erosion or degraded into another condition by general advancement of age of the general land area. The laterite crusts are very suscep-

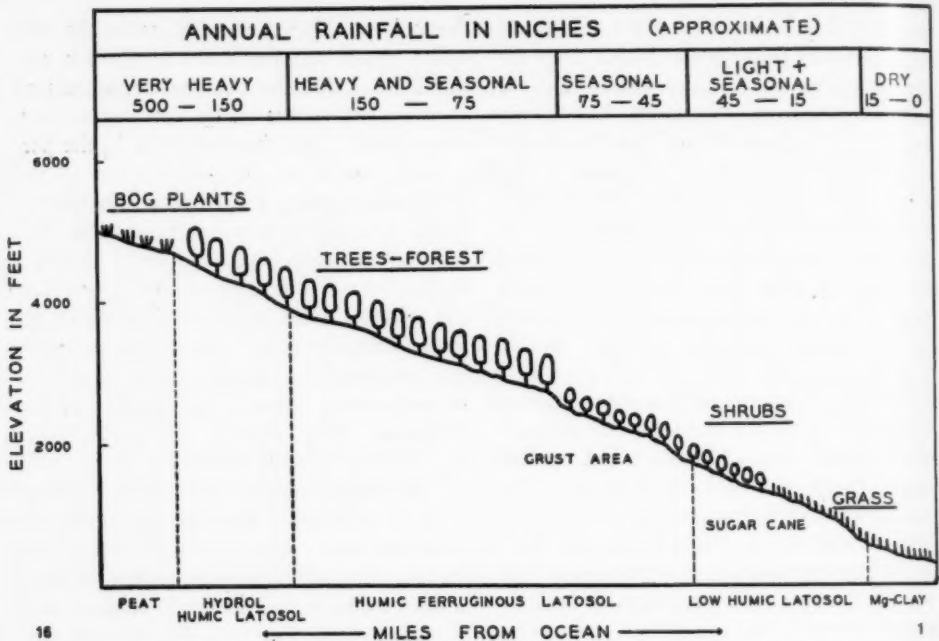


FIG. 1. The location of the ferruginous soils in relation to rainfall distribution, elevation, and vegetation zones.

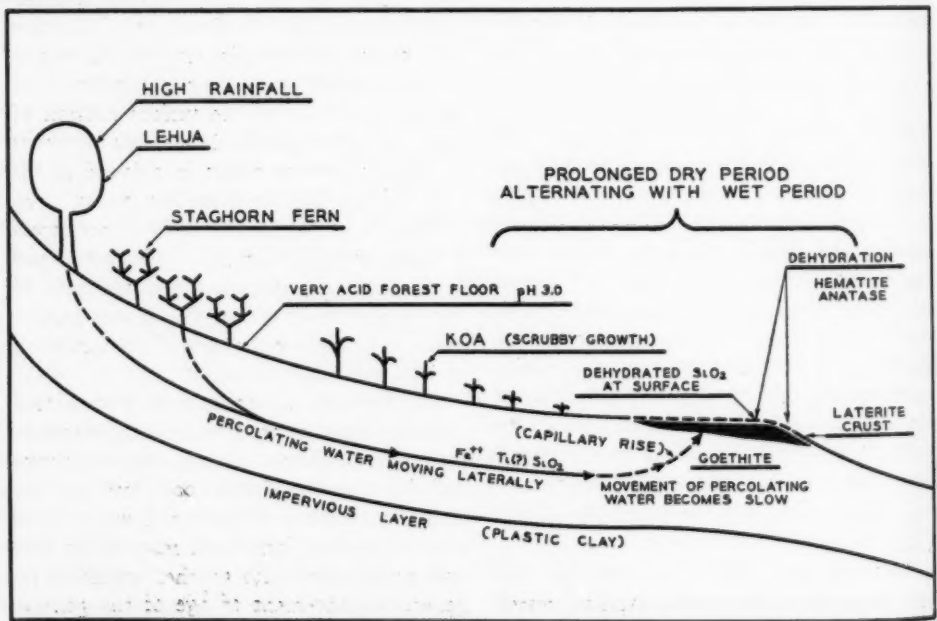


FIG. 2. The location of the ferruginous laterite crust in relation to lateral movement of water from wetter higher elevations.

TABLE 3  
THE CHEMICAL COMPOSITION OF A DEGRADED FERRUGINOUS LATERITE PROFILE  
FROM LIHUE, KAUAI

HORIZON	SiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	TiO <sub>2</sub>
<i>inches</i>	<i>per cent</i>	<i>per cent</i>	<i>per cent</i>	<i>per cent</i>
Former ferruginous crust 6-18	28.5	25.8	9.9	24.4
Former friable layer 22-30	32.0	33.2	13.4	7.6

tible to erosion due to the underlying friable layer. Any break in the crust will permit the initiation of erosion by the removal of the friable soil, thus undermining the hard surface layer. Eventually fragments of the hard surface layer will break off. Erosion will eat rapidly into an area and soon only remnants of the original hard surface will remain. The area found on the white trachyte cliffs of West Maui is a good example of this type of erosion.

When the laterite crust is developed in an area which is becoming nearly a peneplain, that area will undergo degradation. In this case the internal drainage becomes restricted and the soil solum is moist or saturated with water during most of the year. Under these conditions the free iron oxides become unstable and are reduced and leached away in the sluggish percolating waters. Titanium oxide will remain quite stable. The profile becomes enriched with colloidal materials and silica from the slow-moving ground waters of the higher elevations. Thus resilication will take place giving rise to a skeleton crust which is rich in silica, alumina, and titanium oxide and low in iron oxide. A typical analysis of a degraded laterite crust is given in Table 3. The data show an iron oxide content of 9.9 per cent and a titanium oxide content of 24.4 per cent in the surface layer of this former ferruginous laterite crust.

#### SUMMARY

The ferruginous laterite crust has developed in three general areas of the Hawaiian

Islands; namely, the southern and western slopes of leeward Kauai; the westerly slopes of the main mountain range of Molokai; and on the white trachyte cliffs of West Maui. The ferruginous laterite crusts are found on the long slopes which have a region of very high rainfall at the higher elevations and a semi-arid condition at the lower elevations. The areas of ferruginous laterite crusts are located at higher elevations which have a definite alternating wet and dry season.

The ferruginous laterite crust profiles have a hard slaglike surface horizon having a very high apparent specific gravity. This layer is underlain by a friable layer of a thickness varying from 4 to 36 inches. This always lies over an impervious layer of either rock or a plastic clay. The hard surface horizon is rich in iron and titanium oxides and very low in volatile matter. The friable layer is made up of iron oxides, which sometimes constitute as much as 80 per cent of the soil.

A hypothesis is advanced as to the genesis of these ferruginous laterite crusts. This proposes that iron and hydrated titanium oxides in the percolating waters from the soils developed on the wet areas of the higher elevations move laterally over the impervious subsoil layers and subsequently accumulate in the surface horizon by capillary action in regions having an alternating wet and dry season climate. The hydrated iron oxide and titanium oxides are stabilized by dehydration and are converted to hematite and anatase in the surface horizon. This gives rise to a



hard compacted surface horizon with a very high apparent specific gravity.

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# Life History and Feeding Habits of the Giant African Snail on Saipan<sup>1</sup>

W. HARRY LANGE, JR.<sup>2</sup>

THE GIANT AFRICAN SNAIL, *Achatina fulica* Férussac, has recently received considerable attention as an economic threat to the people occupying certain islands included in the Trust Territory of the Pacific Islands because of its catholic taste for fruits and vegetation. In addition, its introduction (but not its establishment, to date) into California on heavy equipment returned from Pacific islands has brought to our attention its status as a potential threat to agriculture in the continental United States.

*Achatina* is very abundant on Saipan, where it causes extensive damage to many types of fruit and vegetable crops. The present study was an attempt to secure additional information concerning its habits, life history, feeding preferences, natural enemies, and seasonal activity. This information may prove of value not only in relation to the possible introduction of natural enemies, but also in determining the economic potentialities of this snail should it ever become established on the mainland of the United States. During this study an opportunity was available to make limited observations of this snail in the Philippines (Luzon), Siam, Malaya, and Java. A survey was made of the other terrestrial and fresh-water snails of Saipan inasmuch as a knowledge of these

species is an important adjunct to a biological or chemical control program.

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## DISTRIBUTION

This is a species which is native to the east coast of Africa, from Natal and Mozambique in the south to Kenya and Italian Somaliland in the north<sup>3</sup> (Mead, 1949:38); from there

<sup>3</sup>Bequaert (personal communication, February 14, 1950) reports that the known distribution is only from northern Mozambique (17° S.) in the south to southern Abyssinia and the southern half of Italian Somaliland in the north (7° 30' N.). Inland it extends 150 to 500 miles from the coast, going farthest inland in the northern section of the range.

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it has spread through many tropical and subtropical areas. It was introduced to Mauritius (1803, or before), later to Seychelles, and about 1847 was introduced to Calcutta, India (Jutting, 1934:43). Several authors report its spread from India (Jarrett, 1931:263; Jutting, 1934:43; and Mead, 1949:38-39). In 1900 it appeared at Ceylon, and in 1911 was present at Singapore and later in other Malayan localities. In Borneo (Sarawak) it appeared in 1928 and in 1933 its presence was noted in Java and Sumatra. It appeared at Amoy, China, in 1931 and was recorded at Hong Kong in 1937.

The Japanese apparently hastened the spread of the African snail during their Pacific campaign because they carried snails as a supplementary diet from one island to another. The snail was undoubtedly present on certain of the islands before the war, but on others had not been introduced. As a result, the snail became more widely distributed in the Dutch East Indies, particularly in New Guinea, New Britain, and New Ireland. It appeared in the Philippines and is known from the Bonin Islands.

In Micronesia, Townes (1946:15-16) reported *Achatina fulica* from Saipan, Tinian, Rota, and Guam in the Marianas and from Koror, Ponape (near Colonia), southern Babelthuap, Peleliu, and part of Truk (Dublon) in the Carolines. T. R. Gardner (personal communication) supplied more detailed information regarding its distribution in the Palau Islands as follows: Angaur, Malakal, Koror, Arakabesan, and the south half of Babelthuap. Mead (1949:39) reported it at Pagan in the Marianas. Reliable natives on Saipan report that the snail has been present on the island for about 10 years. It had also been reported from Pagan prior to the Pacific conflict.

In the Philippines this snail was very common on October 22, 1947, at Los Banos, Luzon, feeding upon papaya fruits. It was found by the writer in southern Siam, north

of Haadjai, on December 8, 1947. In Malaya it was a common, but non-destructive, mollusk in the Port Swettenham region near Klang.

#### DESCRIPTION

The degree of variation in shell size and markings and the internal anatomy of *Achatina fulica* are described by Tryon and Pilsbry (1904-05:55-58).

On Saipan typical shells are dull whitish, yellowish, or gray-tan, with characteristic transverse dark brown to purplish-brown streaks. Transverse dark markings are more prevalent in juvenile specimens. In older individuals the first whorls become white to gray and the body whorl often becomes a uniform tan devoid of transverse markings.

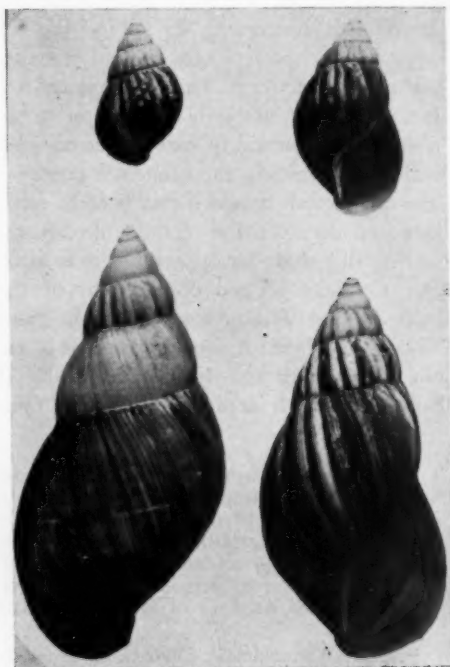


FIG. 1. Shells of *Achatina fulica*; above, juvenile specimens, Saipan, November 3, 1947; below, left, specimen from Rota, March 16, 1948, showing reduction of dark bands; right, typical Saipan specimen, November 3, 1947.

Average specimens are smaller than on Guam, ranging from 2.5 inches to 3.75 inches long. Differences in markings are shown in Figure 1. The shell whorls have transverse striations and microscopic, spiral striae. The animal is gray-tan to black.

Shells often show whitening and, in some individuals, complete loss of color. This condition was quite prevalent on parts of Rota. Many shells show scratching of the surfaces as if caused by burrowing in the soil or by crawling under objects on the surface of the soil. On Saipan an abnormal condition of many shells was observed, namely, the presence of a thin, paper-like shell, easily broken by handling. Shells of normal thickness are found in the same area, but there are areas, such as Marpi Point on the north end of the island, where normal shells are more commonly found. This condition could be a genetic one concerned with carbonate metabolism, or could be a result of the availability of carbonates in particular areas.

#### LIFE HISTORY AND DEVELOPMENT

Inasmuch as the life history and development of the snail on Saipan deviates to some extent from other published reports, a few salient records will be cited. Jarrett (1931:263) reported that in China the African snail laid 100 eggs the first year, 200 to 300 eggs the end of the second year, and produced 1,000 eggs during a 3-year period. He stated that in Malaya egg laying occurred during March, April, and May. The same writer stated that in Borneo eggs were laid in October, and probably throughout the year.

Green (1911:43) concluded that *Achatina fulica* reached full growth in 2 years, but were sexually mature in 1 year, at which time they were about half grown. He did not record a maximum number of eggs, but stated that each snail deposited at least 100 eggs the first year and 500 the second year.

Pilsbry (1919:60-61) described the Acha-

tinae as oviparous, laying as many as 196 eggs in loose soil just beneath the surface.

The fact that *Archachatina marginata* lays eggs in trees is mentioned by Tryon and Pilsbry (1904:205).

D. B. Langford (personal communication) recorded the time interval from egg to sexual maturity as 147 days on Guam. Measurements of Langford's reared specimens on deposit at the Hawaiian Sugar Planters' Association Experiment Station, Honolulu, are tabulated here:

AGE weeks	NUMBER OF WHORLS	LENGTH mm.
1	3	5
2	3.5	8
3	4	12
4	5.5	26
5	6.5	34
6	6.5	40
7	7.5	63

Mead (1949:40) recorded male sexual maturity before the snail is a year old; development of female organs and egg deposition takes a few months longer. The same author also reported retention of the eggs inside the uterus so that eggs hatched within a few hours, but this phenomenon was not observed during the present observations.

On Saipan the eggs are nearly globular, approximately 4 mm. by 5 mm. in size, white when first laid but later turning yellowish. When first laid they are covered with a clear mucus which gives them a glistening appearance. In a few hours the mucus dries and the eggs become a dull white. Eggs are shown in Figure 2.

This snail is hermaphroditic, although reciprocal mating occurs and both individuals lay eggs. Snails mate chiefly at night, but on Saipan mating was continued during the day, particularly if the weather was rainy or overcast. Snails mating under the protection of dense jungle cover or creeping vines often continued to mate during the day. Snails often started to mate in the late afternoon,

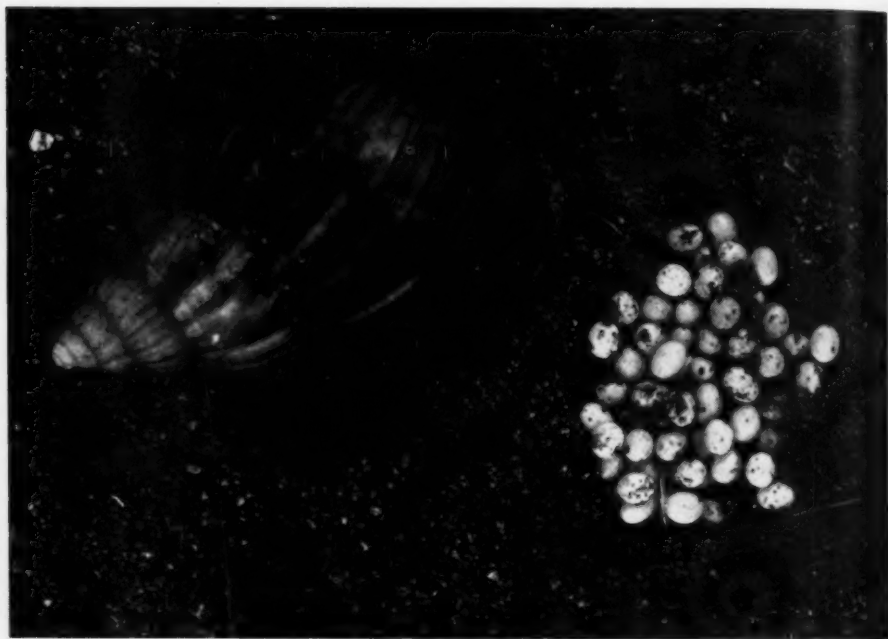


FIG. 2. *Achatina fulica* and eggs, Saipan, October 29, 1947.

and it was noted that individuals crawling about in trees during the day occasionally extruded the genital organs.

In mating one snail usually climbs above another, the organs are interchanged, and both snails fall to one side, remaining together for a period varying from less than 1 hour to 24 hours or more. The manner of mating is shown in Figure 3. Snails collected during coition were held in the laboratory in gallon cans which had been filled with 4 inches of moist soil. After mating, eggs were deposited in from 8 to 20 days, with an average interval of 10 to 12 days. On Saipan a preferred site for egg deposition was under loose soil at the bases of breadfruit trees as shown in Figure 4. Eggs were also laid under rocks, boards, or other objects, or in the soil wherever there was a cover of vines, shrubs, or trees. Eggs were often merely scattered about on the surface of the soil or barely cov-

ered, and rains often exposed many of these. Usually a snail made a depression about 2 inches wide by 1.5 inches deep in loose soil in the ground, deposited its eggs, and covered them with soil.

Egg masses were found in the field from October 16, 1947, to November 11, 1948. The presence of young snails on October 16, 1947, indicated that eggs had been laid prior to this time. The number of eggs laid in the field varied from 93 to 184, with an average of 139 eggs. In the laboratory, egg deposition was observed from October 30, 1947, to November 19, 1947; the eggs were laid in gallon cans filled with 4 inches of soil. The number of eggs laid by individual snails in the laboratory varied from 62 to 243, with an average of 129 eggs.

In captivity most of the snails laid their eggs during one night, but occasionally an



individual would lay a few eggs at a time over a period of several nights.

The length of the egg period in the laboratory on Saipan varied from 6 to 12 days with a mean average period of 8.8 days. In the field the egg period was approximately 11 days. It was noted that under field conditions there was a high incidence of infertility which was not true under laboratory conditions. For this reason failure to hatch under field conditions was attributed to desiccation or other adverse exposure to environmental factors.

After hatching, the young snails began to devour the egg shells and ordinarily remained together in a group feeding on the shells during a 3- to 4-day interval. After this time they scattered, seeking other food. On the day of hatching snails were placed

drinking water was found to affect young snails adversely. During these observations, which extended over a 5-month period, snails increased in size from 2.5 whorls at hatching to 6.5 whorls. Of 20 individuals observed from October 31, 1947, until April 4, 1948, only eight were successfully reared. The following tabulation gives a summary of the information obtained.

TIME EXAMINED	AVERAGE WEIGHT grams	AVERAGE WHORLS number
At hatching	0.04	2.5
25 days	0.22	4.0
60 days	2.14	5.0
121 days	6.37	5.5-6.0
156 days	8.96	5.5-6.5

These rearings are not considered indicative of the rate of growth under field conditions inasmuch as snails were fed irregularly



FIG. 3. *Achatina fulica* mating on ground in jungle area near Klang, Malaya, January 2, 1948.

in cans approximately 4 inches wide by 6 inches deep and growth was observed in the laboratory. They were fed upon pieces of potato or breadfruit, and 1 gram of powdered calcium carbonate was placed in each can to assist in shell formation. Distilled water was used, inasmuch as the ordinary chlorinated



FIG. 4. *Achatina* clustered about the base of a breadfruit tree—a favorite site for egg deposition. Saipan, October 19, 1947.

during a 2-month period when I was in the field. The average weight increase was from 0.04 gram at hatching to 14.7 grams at the end of 156 days. This was an increase in weight of from 63 to 368 times above the initial weight, depending upon the particular snail involved. These rearings suggest that individuals vary greatly in their rate of growth, that weight can be lost when food or water is withheld, and that whorls are added regardless of the presence of adequate food. Mature, pregnant snails were found in the field which were 2.25 to 3.5 inches long, having 7 to 7.5 whorls.

It was noted that under field conditions there was a definite correlation between egg laying and wet and dry periods. Egg laying occurred during the wet season. During the dry season no eggs were laid and many snails secreted brown to whitish epiphragms and became inactive. On October 28, 1947, eight of the 50 snails examined in an area under

breadfruit trees were pregnant. On November 11, 1947, observations made in the same area showed that of several hundred examined only three were pregnant. Of hundreds of snails examined during the period from February 6, 1948, to April 4, 1948, no pregnant snails were found on Saipan. The location of observations apparently influenced the relative percentages of pregnant snails, because, of several hundred snails examined on November 3, 1947, at Marpi Point, Saipan, feeding on *Operculina turpethum* along a roadway, not a single pregnant snail was found. Snails seeking sites for oviposition were found more frequently in more protected areas.

Ordinarily there is a wet and a dry season on Saipan, although this may not be marked inasmuch as rain can fall during any month. There is also considerable variation, depending upon where the observations are made. The wet season is from July to November



FIG. 5. *Operculina turpethum*, a preferred food plant of *Achatina*; Saipan, March 18, 1948.

and the dry season from January to May. The mean average temperature at Tanapag during 1947 varied from 79.7° F. in January to 82.7° F. in August. This small difference would not materially influence activities of the snails. The relative humidity is high all year around, averaging 82 per cent. Records kept at Tanapag during 1947 gave an average of 80 per cent relative humidity during an 8-month period.

Rainfall apparently influences activities of the snails more than any other single factor. The record of the total monthly precipitation at Tanapag during 1947 and part of 1948 is as follows:

MONTH	RAINFALL inches	
	1947	1948
January . . . . .	2.45	4.47
February . . . . .	1.12	1.48
March . . . . .	1.40	3.68
April . . . . .	1.26	4.52
May . . . . .	1.90	2.53
June . . . . .	1.21	3.22
July . . . . .	7.80	
August . . . . .	4.93	
September . . . . .	5.49	
October . . . . .	15.20	
November . . . . .	4.00	
December . . . . .	1.42	

From January to June, 1947, there was a drought in Saipan, and the rainy season extended from July through November. Limited observations made on snail activity indicated that egg-laying periods were definitely correlated with periods of extensive rainfall, although feeding was possible at any time when moisture was present. This was also substantiated by an examination of the internal genital structures. Specimens collected during October and November had a full development of the female organs, whereas in specimens collected from February to April these structures were atrophied.

#### FEEDING HABITS

On Saipan the snail is omnivorous in its feeding habits, but is primarily a scavenger, preferring human and animal excreta, gar-

bage, decaying leaves, rotting fruits, crushed snails of its own kind, and soil. At night the crackling sound caused by the feeding of countless thousands of snails upon decaying leaves can be heard for considerable distances. In one instance 215 snails were counted feeding upon a single decaying breadfruit. Plane runways and roads where snails were crushed by traffic were favorite feeding sites for thousands of snails.

Of the fruits selected by *Achatina*, bananas (also the leaves and new shoots of banana trees), papayas, breadfruit, and ripe passion fruits were preferred. The snail caused severe damage to certain vegetables such as okra, Chinese cabbage, lettuce, melons, and yams. It also fed upon beans, carrots, corn, cucumbers, eggplant, pepper, pumpkins, radishes, squash, and watermelons.

An attempt was made to study the feeding preferences of the snail in relation to other types of vegetation. In general, snails preferred weeds and succulent plants to plants with thick, leathery leaves. In view of these findings the plants listed below will be separated into those preferred and readily eaten and those not readily eaten.

The preferred food plants of the snail on Saipan, together with the Chamorro name (if known) and the family, are listed below:

NAME	CHAMORRO NAME	FAMILY NAME
<i>Annona muricata</i>		Annonaceae
<i>Amaranthus spinosus</i>	kilitis	Amaranthaceae
<i>Albizia lebbbeck</i>		Leguminosae
<i>Asplenium nidus</i>	galag	Polypodiaceae
<i>Blechnum pyramidatum</i>	yerbas babui	Acanthaceae
<i>Canavalia gladiata</i>	gaye	Leguminosae
<i>Cassia occidentalis</i>		Leguminosae
<i>Colubrina asiatica</i>		Rhamnaceae
<i>Grewia mariannensis</i>		Tiliaceae
<i>Ipomoea alba</i>	fofgo	Convolvulaceae
<i>Ipomoea pes-caprae</i>	halai hai	Convolvulaceae

<i>Melanolepis multiglandulosa</i>	alom	Euphorbiaceae
<i>Morinda citrifolia</i>	lada	Rubiaceae
<i>Operculina turpethum</i>	alag-alag	Convolvulaceae
<i>Passiflora foetida</i>	dulce	Passifloraceae
<i>Physalis peruviana</i>	tomates chaca	Solanaceae
<i>Pipturus argenteus</i>	atmahayan	Urticaceae
<i>Portulaca oleracea</i>	bordolagus	Portulacaceae
<i>Tectaria</i> sp.		Polypodiaceae
<i>Thespesia populnea</i>	pago	Malvaceae
<i>Vigna marina</i>		Leguminosae

Of the above plants certain ones are greatly preferred by the snails. These include *Passiflora foetida* (fruit and leaves); certain weeds such as *Blechnum pyramidiatum* and *Physalis peruviana*; creeping vines such as *Ipomoea alba* and *Operculina turpethum* (see Fig. 5); and *Melanolepis multiglandulosa* (which is also a preferred host plant of *Partula gibba*).

Certain plants which are fed upon only occasionally are:

NAME	CHAMORRO NAME	FAMILY NAME
<i>Bikkia mariannensis</i>		Rubiaceae
<i>Callicarpa cana</i>		Verbenaceae
<i>Capparis cordifolia</i>		Capparidaceae
<i>Cerbera manghas</i>	hunig	Apocynaceae
<i>Clerodendron inerme</i>		Verbenaceae
<i>Colocasia esculenta</i>		Araceae
<i>Ficus tinctoria</i>	hodda	Moraceae
<i>Hernandia ovigera</i>		Hernandiaceae
<i>Muntingia calabura</i>		Tiliaceae
<i>Ocrosia mariannensis</i>		Apocynaceae
<i>Ocrosia oppositifolia</i>		Apocynaceae
<i>Pandanus</i> spp.		Pandanaceae
<i>Psychotria mariana</i>		Rubiaceae
<i>Pempbis acidula</i>		Lythraceae
<i>Trema orientalis</i> var. <i>argentea</i>		Ulmaceae

Economic damage to vegetable crops varied from slight damage to complete losses depending upon the kind of crop and its location in relation to adequate diurnal resting places for the snails. Ripe fruits were preferred to green fruits.

#### HABITS

During the latter part of October, 1947, snails were quite active, and the presence of small snails indicated that a major egg-laying period had already been passed. Snails were more active at night although they continued to feed diurnally during overcast or rainy periods. Daytime refuges included trees,



FIG. 6. *Achatina* resting on fence post, Saipan, October 19, 1947. The vine is *Passiflora foetida*, a preferred food plant.

fence posts (see Fig. 6), sides of buildings, rock piles (see Fig. 7), the under surfaces of leaves, boards, and other objects, or dense jungle growth. During favorable conditions snails crawled forth from these protected places to feed. Because of the uneven distribution of refuges, the distribution of snail populations varied and was often concentrated in certain areas. Snails often climbed up into trees to positions 10 to 25 feet above the ground and remained there during the day.

In certain areas on Saipan, Rota, and Tinian, such as plane runways, it was observed that snails often became gregarious and congregated in rather compact masses, as shown in Figure 8. It was thought that this was a method of securing protection and a mechanism of moisture conservation.

It was observed that snails were able to endure lengthy periods without feeding. One snail placed in a cardboard mailing tube lived 5 months without food, except for some of the cardboard lining. The snail died within



FIG. 7. *Achatina* attached to rocks during the day, Mt. Tapachou, Saipan, March 16, 1948. Note loss of apical whorls in one specimen.



a few days after it was dropped and the epiphragm broken. Another snail lived for 5½ months in an outdoor cage without food.

During unfavorable conditions snails were observed to secrete a brown calcareous epiphragm over the aperture. In the field it was noted that certain snails with epiphragms remained in an inactive condition regardless of adequate moisture. In this case it was thought that inactivity was not correlated with wet and dry conditions at the time, but with the physiological condition of the snails or status of development of the female structures.

#### NATURAL ENEMIES

A few natural enemies of *Achatina fulica* are reported in the literature. Green (1911: 43) lists enemies in Ceylon as the common pond tortoise, *Nicoria trijuga* var. *thermalis*; an ant (*Pheidologeton affinis*), which attacks

the eggs; insectivorous birds; and carnivorous beetles.

Bequaert (1925:201; also in Pilsbry, 1919:61-63) records minute, ectoparasitic mites on a living *Achatina* in the Belgian Congo and mentions the wingless flies of the genus *Wandolleckia* (family Phoridae), which live in the adult stage upon the slime of *Achatina*.

Jarrett (1931:263-264) records the Indian firefly, *Lamprophorus tenebrosus* Wlk., as an important parasite of young *Achatina fulica*.

In the Marianas no effective natural enemies of the giant snail were observed, and the toad *Bufo marinus*, supposedly introduced to feed upon snails, took no appreciable toll. On March 13, 1948, a few snails on Saipan and Tinian were found in a moribund condition although the cause of sickness was not determined. The bodies of the snails became



FIG. 8. Aggregation of *Achatina* on Tinian airstrip, March 13, 1948. Several hundred snails were found in an area of approximately 54 square inches.

lighter, receded into the shells, then became black, and finally a watery, dark-colored liquid exuded from the apertures. From dying and dead snails two species of sarcophagids were reared, namely, *Sarcophaga gressitti* Hall and Bohart and *S. dux* Thomsen (determined by C. W. Sabrosky). These flies were apparently saprophagous, being attracted to dying snails. Hall and Bohart (1948:132) report *Sarcophaga gressitti* from Saipan, Tinian, and Rota, where it was associated chiefly with filth, dead fish, dead land crabs, and snails.

During these observations there was no evidence of an epizootic among snails; rather it appeared that dying snails were stranded on roads and runways and partially desiccated before they could obtain adequate cover. This does not, however, preclude the possibility of a pathological condition among snails in other areas or under other conditions.

The presence of thin and consequently

fragile shells among snails on Saipan, Tinian, and Rota did not seem associated with a pathological condition. The possibility of genetic factors is indicated in certain Saipan localities where normal thick-shelled individuals occurred in association with thin-shelled snails. In certain cases, as on Rota (Fig. 9), the bleached shells of dead snails were found in large numbers. The reason for the death of these snails could not be determined.

#### CONTROL

The control of the giant African snail on Saipan has been approached in three ways: by chemical control, cultural control, and biological control. In certain cases it was possible to protect crops by the frequent use of pelleted baits containing metaldehyde and calcium arsenate. In areas separated from dense growth the use of a peripheral weekly treatment with pellets was found to give sat-



FIG. 9. Bleached shells of dead *Achatina* on Rota airstrip, March 16, 1948.

isfactory protection. Extensive chemical control methods in rocky or dense terrain would probably be of only temporary value unless new and more specific chemicals could be developed. The developments in new chemicals would probably have to be a divergence from related aldehydes, as was shown by the work of Lange (1941:321) in which chemicals related to metaldehyde were found to have no attraction for slugs and the European brown snail.

Cultural methods had definite value. Clearing dense underbrush near gardens or field plantings was found to be of value, as was the elimination of piles of refuse or other places where snails could hide during the day.

The work of Dr. F. X. Williams in Africa, reported by Mead (1949:41), revealed two predatory snails (*Gonaxis* sp. and *Edentulina* sp.) which may prove of value, but they require special investigation before they can be liberated. Most terrestrial predatory snails, unless they have a reproductive potential greater than *Achatina* or a decided specificity for *Achatina*, probably would not be entirely satisfactory in reducing large populations of the giant snail. This conclusion would also apply to the large predacious carabid beetle, *Tefflus* sp., found by Dr. Williams in Africa.

#### OTHER TERRESTRIAL SNAILS

In a control program it is necessary to recognize other terrestrial or fresh-water mollusks present in an area, and to know their distribution and ecological relationships. A complete survey was not made, but the following list shows present knowledge concerning these other species found in the Marianas Islands:

LOCALITY AND DATE COLLECTED	SPECIES	DETERMINER
Magicienne Bay, March 18, 1948	<i>Lymnaea (Fossaria) ollula</i>	Abbott

Loa Loa, March 11-12, 1948	<i>Lamprocystis</i> sp.	Lange	
	<i>Omphalotropis cookei</i>	Lange	
	<i>Omphalotropis erosa</i>	Kondo	
	<i>Omphalotropis submaritima</i>	Kondo	
	<i>Pytbia intermedia?</i>	Kondo	
	<i>Subulina octona</i>	Kondo	
	<i>Succinea</i> sp.	Kondo	
	<i>Truncatella querini</i>	Kondo	
	Mt. Nafutan, March 12, 1948	<i>Gastrocopta lyonsiana</i>	Abbott and Kondo
		<i>Lamellaxis gracilis</i>	Abbott
<i>Lamprocystis misella</i>		Kondo	
<i>Omphalotropis conica</i>		Kondo	
<i>Omphalotropis cookei</i> (type locality, Abbott, 1949:263-66)		Abbott	
<i>Omphalotropis erosa</i>		Kondo	
<i>Pytbia</i> sp.		Kondo	
<i>Succinea piratorum?</i>		Kondo	
<i>Succinea</i> sp.		Kondo	
<i>Synopeas javanicum?</i>		Kondo	
Marpi Point, March 4, 1948	<i>Truncatella querini</i>	Kondo	
	<i>Diplommatina taeneolata</i>	Abbott and Kondo	
	<i>Georissa biangulata</i>	Abbott	
	<i>Lamprocystis</i> sp.	Abbott	
	<i>Nesopupa quadrasi</i>	Kondo	
	<i>Omphalotropis erosa</i>	Kondo	
	<i>Omphalotropis submaritima</i>	Abbott	
	<i>Paludinea conica</i>	Abbott	
	<i>Partula gibba</i>	Abbott and Kondo	
	<i>Succinea</i> sp.	Abbott	
Marpi Point, March 18, 1948	<i>Lamellaxis</i> sp.	Lange	
	<i>Omphalotropis cookei</i>	Lange	
	<i>Omphalotropis</i> sp.	Lange	

Mt. Tapachou, April 2, 1948	<i>Bradybaena (Eu- lota) similaris</i>	Kondo
	<i>Lamprocystis fastigata</i>	Kondo
	<i>Partula gibba</i>	Abbott
N.E. Saipan, April 2, 1948 (fresh-water spring)	<i>Lymnaea (Fossa- ria) ollula</i>	Abbott

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## Notes on Amblypygi Found in Territories Adjacent to Japan

HARUO TAKASHIMA<sup>1</sup>

THE PEDIPALPI form an order of arachnids found throughout Asia, the Australian islands, and the tropical and subtropical regions of Africa and North and South America. This order contains about 160 species, divided into 3 families and 26 genera. The majority of them are found in India, the Indo-Malayan region, Central America, and northern South America. These two major concentrations in the Old and the New Worlds appear to be the centers of dispersions for the Pedipalpi.

Some species are quite small, so small that they can hardly be seen by the naked eye. Consequently, many of them have little interest to our daily lives. However, this group is very interesting scientifically and attracts the attention of many arthropodologists.

The Amblypygi, one of the several families of the Pedipalpi, is subdivided into 3 subfamilies, 13 genera, and about 53 species which inhabit the tropical and subtropical regions of Asia, Africa, America, and some of the neighboring islands of Australia. Their appearance is somewhat grotesque, but they are harmless and not to be feared, having no poison or strong biting jaws. Amblypygi have the following diagnosis: carapace much wider than its length; edge of abdomen round with no caudal appendage; tarsi of first pair of legs extraordinarily long and slender with many joints.

Among the 13 known genera, *Charon* Karsch, 1879, alone is found in territories adjacent to Japan. It has the following diagnosis: the tibia of the pedipalps is not broadly

extended; the upper ridge of the tibia has two long spines which are almost the same length and much longer than those of the other tibia; its hand has only one long spine on each of the upper and lower ridges; there are two to four small spines on the anterior part of the long spine, and they become gradually longer near the apex. Fingers are not segmented and usually have no spines, but if they are present, only minute ones are seen at the proximal end. The corrugation on the abdomen is clearly visible at the margin of the second abdominal sternum. Of these characteristics, the most useful in distinguishing this genus from all others is the absence of joints in the fingers.

Some authors divide this genus into several species, but I consider it monotypic, with a single species known as *Charon grayi* Gervais, 1844. Furthermore, I do not think it is necessary to recognize subspecies, for variations are individual and not worthy of such recognition. I propose to call this species "Kan'imushi Modoki" in Japanese.

*C. grayi* is found in the Malay Peninsula, Java, the Philippines, Bonaire, Tobago (or Kōtōsho near Formosa), Sumbawa, Amboina, New Guinea, the Bismarks, and the Solomons and Palau (Pelew) in Micronesia; it appears rare in the Malay Peninsula, while rather common in the Philippines, Manila being its type locality.

Amblypygi were reported for the first time from Micronesia by Dr. T. Esaki (1936) who obtained a male, a female, and a juvenile on the island of Peleliu in the Palau group. Since that time this animal has been found occasionally in the Palau group—as far as I

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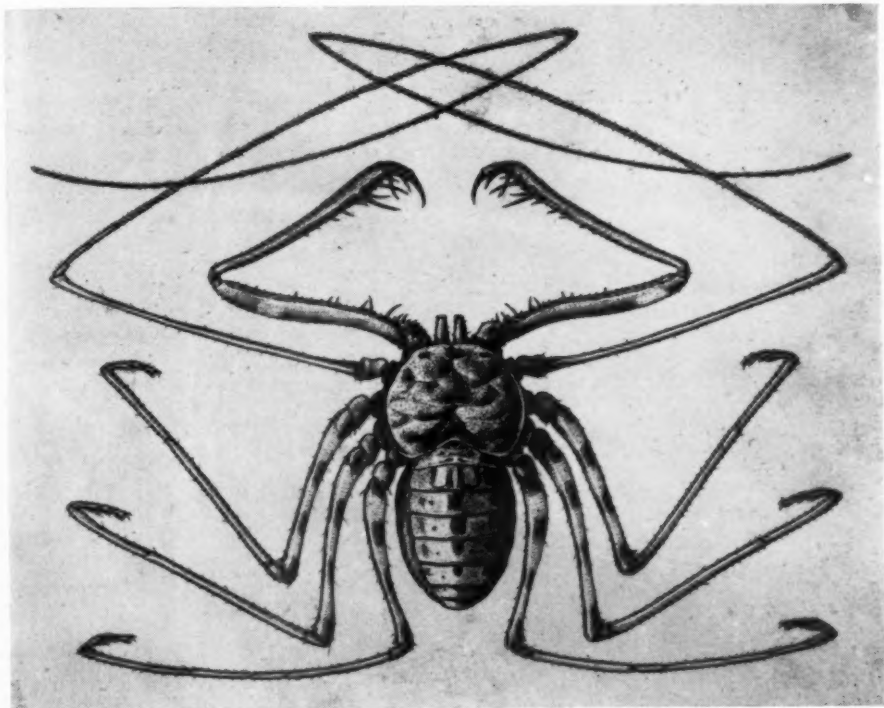


FIG. 1. Dorsal view of *Charon grayi*, female, from Botel Tobago, near Formosa. After Kano.

can ascertain, we have counted 11 examples—nevertheless it seems uncommon there. The fact that, in Micronesia, it is found only in the Palau Islands shows a close zoogeographical affinity of these islands to New Guinea and the Philippines. Fortunately I now possess 4 specimens of the 11 that have been obtained in Micronesia.

In 1936, the same year in which Dr. Esaki obtained his specimens, Dr. Kano, an able Japanese biogeographer (unfortunately missing since the war), found this species in a stalactite grotto on Botel Tobago and published an account of it in the following year. Four of his specimens were given me, and, to the best of my knowledge, these are all the Botel Tobago specimens in existence today. I am further fortunate enough to have had an opportunity to examine specimens

from Mindanao, Java, and Bougainville Island. In these various specimens, I am able to detect a secondary sexual character in this species. The femur of the pedipalp in the male is longer than the second, the third, and the fourth pairs; in the female, the femur of the pedipalp is quite similar to those of the other three. I believe this is the most easily distinguishable secondary sexual character in this species.

During the breeding season, the female of this species has an egg-sac on its abdomen. One of the two specimens which Mr. K. Sekiguchi captured on Koror in the Palaus was only 7 mm. long, which led me to believe that the one whose body measuring about 10 mm. was still in a juvenile stage. Yet I found later that it already carried an egg-sac, so I concluded that it must be an adult. This



FIG. 2. *Charon grayi* from Palau. Male, above; female with egg-sac, below. Photo by the author.

particular specimen has only seven eggs in a single layer in the sac, which measures 7 mm. across. A Javanese specimen 25.5 mm. long, in my possession, has more than 80 eggs in several layers in a sac 14 mm. long. An egg of the Javanese specimen is larger than one

of the small Micronesian adults which I have just mentioned. I consider that the diminutive adult 7 mm. long, which looks like a juvenile at first glance, is already matured, and that the animal grows to a larger size, even to the size of the Javanese specimen, as it lives and reproduces. One other specimen from Koror measured only 6 mm. long but, inasmuch as it shows the secondary sexual characters stated above, it must be concluded that it is a female.

In this present contribution I have not mentioned the body length, width of carapace, and second abdominal sternum, which also contribute to determining the secondary sexual characters of this species, but the description I have given suffices to distinguish the sexes.

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## The Subgenera of *Dubautia* (Compositae): Hawaiian Plant Studies 18<sup>1</sup>

HAROLD ST. JOHN<sup>2</sup>

### THE SUBGENERA OF *Dubautia*

THE SHRUBBY or arborescent Compositae of the Hawaiian Islands have attracted much attention and study. Among them are the related genera *Dubautia* and *Railliardia*, early described by Gaudichaud and maintained by nearly every investigator to the present. They were separated by characters of the involucre, paleae, and pappus. Many of the botanists who have done field work in Hawaii got their first concept of *Dubautia* from *D. plantaginea*, a vigorous small tree of the mountains of Oahu. Its involucre of 4 to 6 firm distinct bracts and its terminal plume of crowded oblong-ob lanceolate leaves, glabrate on the surfaces, give it a very marked habit and aspect. In *Railliardia* there are numerous species—small bushes with sessile and coriaceous, often decussate, leaves which clothe the stem for a considerable distance. The involucre is cylindrical or campanulate, of several involucral bracts united into a tube. Once formed, it is difficult to break away from this concept of the two old genera, but *R. arborea* Gray and *R. struthioloides* Gray are trees; and *R. lonchophylla* Sherff, though a shrub

only 3 to 4 feet tall, has foliage similar to that of *D. plantaginea*. Thus, if all the known species are examined, it is evident that there can be no consistent groupings of the species into several genera on the basis of stature, foliage, or involucre.

In a review of *Dubautia* and *Railliardia*, Keck (1936: 24–25) emphasized the existence of species invalidating each one of the several characters alleged to separate the two genera. The two genera had recently been monographed, but Keck asserted (p. 25) that the monographer "Sherff gives an admirable systematic account of the species, but evades the question of how the two genera are to be distinguished by failing to raise it."

To one acquainted with the plants in the field there is no habitual aspect to separate the species into two groups and, as indicated, there are no strong morphological differences, not even a single constant character. Keck's merging of the two genera has not been generally adopted, inasmuch as the following botanists have continued in the maintenance of both *Dubautia* and *Railliardia*: Sherff (1941: 29–30); Degener (1940 and 1946); and Selling (1947: 330–332), who gave the first detailed account of the pollen of the Hawaiian plants. Selling accepted both *Dubautia* and *Railliardia* (= *Railliardia*), and, referring (p. 331) to Keck's reduction, said "there seems to be no proper reason for this." Selling describes and illustrates pollen of the two genera, describing it in almost identical phrasing. He states that one cannot separate *Railliardia* from *Dubautia* on the basis of structure of the pollen grains. This might sound like a significant fact, but also inseparable on the basis of pollen structure, are the

<sup>1</sup>This is the eighteenth of a series of papers designed to present descriptions, revisions, and records of Hawaiian plants. The preceding papers have been published in *Bernice P. Bishop Mus., Occas. Papers* 10(4), 1933; 10(12), 1934; 11(14), 1935; 12(8), 1936; 14(8), 1938; 15(1), 1939; 15(2), 1939; 15(22), 1940; 15(28), 1940; 17(12), 1943; *Calif. Acad. Sci., Proc.* IV, 25(16), 1946; *Torrey Bot. Club, Bul.* 72: 22–30, 1945; *Lloydia* 7: 265–274, 1944; *Pacific Sci.* 1: 5–20, 1947; *Brittonia* 6(4): 431–449, 1949; *Gray Herb., Contrib.* 165: 39–42, pl. 3, 1947; *Pacific Sci.* 3(4): 296–301, 1949.

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genera *Lagenophora*, *Tetramolopium*, *Argyroxiphium*, and other genera with the "*Dubautia* type pollen." So, at least, the pollen structure provides no significant differences between *Dubautia* and *Railliardia*. Selling twice accompanied Skottsberg on field trips to the Hawaiian Islands and Selling's rejection of Keck's work seems in harmony with that of his elder companion, Skottsberg. Skottsberg (1944: 510) discounted Keck's revision. He discussed Keck's evaluation of the characters and consequent fusing of the two genera under *Dubautia*, and said, "I cannot find, however, that he has brought to light any new circumstances, not known to Hillebrand, Sherff, Degener and other writers on this subject, and they have considered it better to keep them separate. Nothing is gained by uniting them." Then Skottsberg described a new species of *Raillardia* [= *Raillardia*]. To this it may be replied that the gain attained by Keck is the delimiting of a genus with diagnostic characters that can be stated in words by one botanist and applied with the same understanding by others. The reduction of *Raillardia* to *Dubautia* is here accepted. The only recent authors accepting the view of Keck seem to be Hartt and Neal (1940: 264), Fosberg (1943: 395-397 and 1948: 115), and Neal (1948: 743). Fosberg, in his "Summary of the Hawaiian Seed Plants," places *Raillardia* as a synonym of *Dubautia* and indicates that it is a descendant of the original immigrant *Argyroxiphium*.

Of the several characters previously used for generic separation, the best and most significant are those of the freedom or union of the involucre bracts and the degree of ciliation of the pappus. Both of these characters are significant and have always been used in the classification of these species into larger groups. However, the two pairs of characters are not always correlated. Six species have the involucre of separate bracts, and the pappus awns short ciliate lacerate or short ciliate, these representing *Dubautia* of Gaudichaud.

Twenty species have the involucre bracts united into a campanulate or funnel-form involucre, and the pappus awns long plumose, these representing *Raillardia* of Gaudichaud. There remain three species, all from Kauai, which have the involucre campanulate, united for from  $\frac{1}{4}$  to  $\frac{3}{4}$  of its length, and the pappus awns short ciliate. These three perfectly recombine the characters of the two older groups. As they cannot be logically fitted into either of these groups, a new subgenus, *Mixta*, is made to receive them; the other two groups are described as subgenera.

Keck removes the Hawaiian genera *Dubautia* and *Raillardia* from the Madieae and, quoting Bentham's opinion, refers to their being likened to *Robinsonia* and *Rbetinodendron* of Juan Fernandez. The similarity is in their habit of growth as small rosette trees, but in characters of flowers and fruit there are fundamental differences from these genera of the Senecioneae. Keck inclines towards the views of Skottsberg that close relatives are *Bedfordia* of Australia and *Brachionostylum* of New Guinea. These are both of the Senecioneae, and, on analysis of their characters, are markedly different. *Bedfordia* is a genus of two species of Tasmania and Victoria in Australia—shrubs or trees with stellate tomentose leaves, heads axillary or in axillary panicles, and the denticulate capillary pappi very numerous and caducous. *Brachionostylum* is a monotypic genus from the high mountains of southwest New Guinea—a shrub with the heads unisexual, heterogamous, anthers free, and the pappus bristles slender, capillary, roughened, and early caducous. On comparison, neither of these genera has the habit, or similarity of flower and fruit structure, to suggest that it is a close relative of *Dubautia*.

Keck agrees with the Engler and Prantl system in placing the Hawaiian *Dubautia* and its relatives in the Heliantheae-Galinsoginae; that seems the best placement at present, though by its structure and habit it is not a

close relative of the other genera currently assigned to that subtribe, and those species with a smooth receptacle wholly lacking chaff are least satisfactorily placed there. Hence, the fact that all the other genera placed there are American does not necessarily imply that *Dubautia* is of American parentage. The Galinsoginae are a group transitional to the Helenieae. The Senecioneae also has to be considered, and it is worthy of note that in the Engler and Prantl key to the Compositae the old genera *Dubautia* and *Raillardia* are included in the keys of all three of these tribes. Investigations in search of a closely related genus have been made in these three tribes, but the writer must report that he failed to find one.

#### Key to Subgenera of *Dubautia*

- Involucral bracts distinct; pappus bristles short ciliate or lacerate-ciliate . . . *Eudubautia*  
 Involucral bracts united for part of their length,  
 Pappus bristles long plumose . . . . .  
 . . . . . *Raillardiaster*  
 Pappus bristles short ciliate . . . *Mixta*

#### Genus DUBAUTIA Gaud.

##### Subgenus *Eudubautia* subgen. nov.

*Dubautia* Gaud., Voy. Freycinet Uranie, Bot. 469, (1826) = 1830; Atlas pl. 84, 1826.

Type species: *D. plantaginea* Gaud., l. c.

Bractae involucri liberae. Aristae pappi ciliati-laceratae vel brevis ciliati.

Bracts of the involucre distinct. Pappus bristles squamose, ciliate-lacerate, or usually short plumose.

##### Enumeration of Species

- Dubautia Knudsenii* Hbd., Fl. Haw. Is. 223, 1888.  
*D. laxa* H. & A., Bot. Beechey Voy. 87, 1832.  
*D. laevigata* Gray, Amer. Acad. Arts and Sci., Proc. 5: 135, 1861.

*D. magnifolia* Sherff, Amer. Jour. Bot. 20: 616, 1933.

*D. microcephala* Skottsbl., Hort. Gotoburg., Acta 2: 277-280, fig. 8, 1926.

*D. plantaginea* Gaud., Voy. Freycinet Uranie, Bot. 469, (1826) = 1830; Atlas pl. 84, 1826.

##### Subgenus *Raillardiaster* subgen. nov.

*Raillardia* Gaud., Voy. Freycinet Uranie, Bot. 469, (1826) = 1830; Atlas pl. 83, 1826.

Type species: *R. linearis* Gaud., l. c.

Bractae involucri cohaerentae, involucrem tubulosum vel anguste campanulatum infundibuliformeve est. Aristae pappi longe plumosae.

Bracts of the involucre united into an involucre tubular or narrowly campanulate or funnellform. Pappus bristles usually long plumose.

##### Enumeration of Species

*Dubautia arborea* (Gray) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.

*Raillardia arborea* Gray, Amer. Acad. Arts and Sci., Proc. 5: 134, 1861.

*D. ciliolata* (DC.) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 26, 1936.  
*Raillardia ciliolata* DC., Prodr. 6: 441, 1837.

*D. coriacea* (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia coriacea* Sherff, Bot. Gaz. 95: 80, 1933; later as *Raillardia coriacea* Sherff, Bernice P. Bishop Mus., Bul. 135: 122, 125, fig. 40, 1935.

*D. demissifolia* (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia demissifolia* Sherff, Bot. Gaz. 95: 78, 1933; later as *Raillardia demissifolia* Sherff, Bernice P. Bishop Mus., Bul. 135: 118-120, fig. 38, 1935.



- D. Hillebrandi** (Mann) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936 (as *D. Hillebrandii*).  
*Raillardia Hillebrandi* Mann, Amer. Acad. Arts and Sci., Proc. 7: 175, 1867 (as *Raillardia Hillebrandii* Mann in Sherff, Bernice P. Bishop Mus., Bul. 135: 126, 1935).
- D. kohalae** (Skottsb.) comb. nov.  
*Raillardia Kohalae* Skottsb., Hort. Gotoburg., Acta 15: 510-511, 1944. The specific name is a geographic one, taken from the type locality in the Kohala Mts., and hence, following Rec. XLIII of the International Rules, should be written with a small initial letter.
- D. latifolia** (Gray) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 26, 1936.  
*Raillardia latifolia* Gray, Amer. Acad. Arts and Sci., Proc. 5: 132, 1861.
- D. linearis** (Gaud.) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia linearis* Gaud., Voy. Freycinet Uranie, Bot. 469, (1826) = 1830; Atlas pl. 83, 1826.
- D. lonchophylla** (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia lonchophylla* Sherff, Amer. Jour. Bot. 20: 619, 1933; later as *Raillardia lonchophylla* Sherff, Bernice P. Bishop Mus., Bul. 135: 122, fig. 39, 1935.
- D. Menziesii** (Gray) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.  
*Raillardia Menziesii* Gray, Amer. Acad. Arts and Sci., Proc. 5: 133-134, 1861.
- D. molokaiensis** (Hbd.) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia Molokaiensis* Hbd., Fl. Haw. Is., 226, 1888.
- D. montana** (Mann) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.  
*Raillardia montana* Mann, Amer. Acad. Arts and Sci., Proc. 7: 176, 1867.
- D. platyphylla** (Gray) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.  
*Raillardia platyphylla* Gray, Amer. Acad. Arts and Sci., Proc. 5: 134, 1861.
- D. reticulata** (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.  
*Raillardia reticulata* Sherff, Bot. Gaz. 95: 78, 1933; later as *Raillardia reticulata* Sherff, Bernice P. Bishop Mus., Bul. 135: 128, 130, fig. 41, 1935.
- D. Rockii** (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.  
*Raillardia rockii* Sherff, Bot. Gaz. 95: 79, 1933; later as *Raillardia Rockii* Sherff, Bernice P. Bishop Mus., Bul. 135: 130-131, 1935. The change from *R. rockii* to *R. Rockii* was made by Sherff himself in his second discussion of the species. Though he quoted the original specific name incorrectly as *Rockii*, still this second one is an acceptable form of a personal specific name, and it can be adopted as a correction by the author himself of a typographical error.
- D. scabra** (DC.) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 26, 1936.  
*Raillardia scabra* DC., Prodr. 6: 441, 1837.
- D. Sherffiana** Fosb., Torrey Bot. Club, Bul. 70: 395-397, 1943. (See fig. 1.)
- D. struthioloides** (Gray) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 28, 1936.  
*Raillardia struthioloides* Gray, Amer. Acad. Arts and Sci., Proc. 5: 134, 1861.
- D. ternifolia** (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia ternifolia* Sherff, Amer. Jour. Bot. 20: 618, 1933; later as *Raillardia ternifolia* Sherff, Bernice P. Bishop Mus., Bul. 135: 121, 1935.
- D. thyrsoiflora** (Sherff) Keck, Bernice P. Bishop Mus., Occas. Papers 11(19): 27, 1936.  
*Raillardia thyrsoiflora* Sherff, Amer. Jour.

Bot. 20: 618, 1933; later as *Railliardia thyrsoiflora* Sherff, Bernice P. Bishop Mus., Bul. 135: 121-122, 1935.

Omitted from this enumeration of species are numerous described varieties and forms. Also omitted are the several interspecific hybrids and intergeneric hybrids described by Sherff or by Degener and Sherff. These putative hybrids have not been evaluated and allocated by the writer.

#### Subgenus *Mixta* subgen. nov.

Type species: *Dubautia railliardioides* Hbd.; the reference follows.

Bractea involucri plusminusve cohaerentae, involucrem campanulatum est. Aristae appi brevi ciliati.

Bracts of the involucre more or less united; involucre campanulate; pappus bristles short ciliate.

#### Enumeration of Species

*Dubautia paleata* Gray, Amer. Acad. Arts and Sci., Proc. 5: 135, 1861.

*D. railliardioides* Hbd. (as *D. raillardioides*), Fl. Haw. Is. 224, 1888, emend. Sherff, Bernice P. Bishop Mus., Bul. 135: 107, 1935. Hillebrand published his new species as *D. raillardioides* and discussed its similarity to the next genus, *Raillardia* of Gaudichaud. We must accept this generic name as *Raillardia*, which was the original, well-formed, and valid name. Hence, though there is no covering rule, Sherff took the logical, and, we believe, correct course in changing the specific name to be in harmony with the correct spelling of the generic name. He was not justified in capitalizing the specific name *D. railliardioides* under the 1935 International Rules of Botany, Rec. XLIV, examples, and Art. 3.

*D. waialeale* Rock, Torrey Bot. Club, Bul. 37: 303-304, f. 5, 1910.

#### NOTES ON *Dubautia Sberffiana*

The type collection of *Dubautia Sberffiana* Fosb. is *H. St. John & F. R. Fosberg 12,161*, from Oahu, Waianae Mts., brushy ridge, east of 2nd gulch east of Kaupakuhale, Mokuleia, 2,500 ft. alt., Oct. 23, 1932. At the same time and locality, only 200 feet higher up the same ridge, another collection of this novelty was made (*St. John & Fosberg 12,162*); but this was not listed in Fosberg's paper.

The species of the subgenus *Railliardiaster* are not common on Oahu, and not until September 18, 1949, did the writer find another colony. When climbing one of the narrow rocky ridges leading to Puu Kanehoa in the Waianae Mountains, he saw below him a patch of unfamiliar yellow flowers. By grasping hands with a student he was lowered over the brink and he grabbed a few sprigs of what appeared to be *Railliardiaster*. Returning the next week, he was roped by his companions, M. Canoso and C. E. St. John, and lowered 20 feet down the vertical basalt cliff. There, on a dirt covered ledge so narrow as to deny a foothold to man, were three vigorous bushes 1-1.5 meters tall, many-branched, with the numerous cymes in full golden flower. After taking photographs and gathering full specimens, the collector was hauled again to a foothold on the knife-edged ridge. The data for these specimens are: Oahu, Waianae Mts., southeast ridge of South Peak of Puu Kanehoa, on face of basalt cliff, 20 ft. below crest of sharp ridge, 2,600 ft. alt., in open sunny spot, at top of thicket of *Metrosideros* and *Euphorbia*, Sept. 25, 1949, *H. St. John 23,924*; and also, *23,922* and *23,923*. Though collected in the southern part of the Waianae Mountains, these specimens proved to be of the same species, *Dubautia Sberffiana* Fosberg, earlier described from the northern part of the range. After studying all of the specimens, including an isotype, the following changes in description are proposed: blades



FIG. 1. *Dubautia Sherffiana* Fosb. a, habit  $\times \frac{1}{2}$ ; b, leaf  $\times 1$ ; c, achene with pappus  $\times 5$ ; d, involucre and flowers  $\times 5$ . From *St. John* 23,924.

5(-7)-nerved; pappus bristles 16-25 in number, 2.5-3.5 mm. long.

Though the subgenus *Raillardiaster* is rare on Oahu, there are to be considered two published records of its occurrence. Sherff (1935: 113) summarizes the range of *Raillardia scabra* as "Hawaii, Maui, and Oahu." This species is common and Sherff lists nearly a whole page of specimens, but no collection from Oahu is in his list. None is in the Bishop Museum; nor has any other published record been seen, so Sherff's record seems to be an error.

Sherff also lists (1935: 125-126) *Raillardia linearis* Gaud. as on "eastern Maui, western Oahu, Lanai, and Hawaii." For Oahu he cites, U. S. Exploring Expedition, Kaala (Waianae) mountains, Oahu, 1840 (Gray, New York). Since 1840 no other collector has found this species on Oahu, but many have done so on the three more southerly islands. The flora of Oahu is the best known of any island in the group and its montane flora is well preserved. The U. S. Exploring Expedition also obtained specimens of this species on Maui and Hawaii. This expedition was large and well organized but inharmonious. The commander, Capt. Charles Wilkes, had trouble with his officers on the trip and after it, and with the scientists for decades afterwards while acting as editor of the publications of the expedition. In the botanical collections made by this expedition, it is now known that there is much confusion, as often the loose labels with the data were inserted with the wrong specimens. Piper (1906: 15) discussed this in detail, and the evidence is well known. It is probable that the U. S. Exploring Expedition specimen came not from Oahu, but from Maui or Hawaii with their other collections of these species. In any case, their record from Oahu is questionable until confirmed by a well-substantiated collection.

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Descriptions of Some Species of the Genus *Pulvilligera*  
Strand from the South and Southwest Pacific  
(Hymenoptera: Chalcidoidea; Torymidae)

H. E. MILLIRON<sup>1</sup>

STRAND (1911) proposed the tribe Pulvilligerini based on a new monobasic genus, *Pulvilligera*, the type of which is *P. maxima*, described by him in the same paper from six males collected by H. Sauter in 1908 at Taihanroku, Formosa. He made use of the key to the tribes of Toryminae (= Callimominae) published by Schmiedeknecht (1909), obviously without being aware of the error therein, which described the tribe Megastigmini as having one calcar on the hind tibia, instead of two that the group really possesses. If Strand had realized this fact, he would probably have placed *P. maxima* in the tribe Megastigmini, because its close affinity with the Megastigmini, except for this one character, was clearly indicated at the time he proposed the new names.

Crawford (1914) treated Pulvilligerini as a subfamily without having seen *P. maxima*. In his key, Pulvilligerinae was differentiated from Megastigminae only on the basis of "whorls of hair" on the male antennae. The identity of the Pulvilligerinae has remained completely obscured and unrecognizable for many years. Girault (1915) stated that there "is an undescribed genus in this group [Megastigmini] like *Megastigmus* but the male antennae are very slender and with whorls of hair," but he had not obtained females with certainty. In 1928 the same worker described a species which he placed in the genus *Pulvilligera*.

During 1944 a long series of specimens, part of which appear to represent the same

species described by Strand from Formosa, was collected on one of the Solomon Islands. In a recent publication by the writer (1949) the Pulvilligerinae were omitted from the key (p. 259) pending further study of *P. maxima* as well as of the two new species that are described later in this paper. This study has led to non-recognition of the name Pulvilligerini and of the subfamily name based on it. It is proposed here to treat *Pulvilligera* merely as a genus of the tribe Megastigmini.

While the male antennae of the three species at hand are distinctly different from those of any other known megastigmine species, the females are very much like those of other species of the genus *Megastigmus*. The value of this antennal character of the male as a basis for the recognition of tribal and subfamily groups is extremely doubtful because males of different species within several chalcidoid genera may exhibit striking differences in appearance of the antennae.

*Acknowledgment:* The writer gratefully acknowledges the kindness of Mr. C. F. W. Muesebeck, Chief of the Division of Insect Identification, U.S.D.A., who made it possible to study this material at the U. S. National Museum.

Tribe MEGASTIGMINI

Genus PULVILLIGERA Strand

*Pulvilligera* Strand, Ent. Rundschau 28: 59, 1911. Monobasic. Type: *P. maxima* Strand.

Species of this genus differ from those of the typical genus as follows:

<sup>1</sup>Glendale, West Virginia. Manuscript received March 31, 1950.



*Male:* Antenna slender with distinct three-segmented club bearing short, thick, almost recumbent pubescence; funicle with segments of nearly equal length, each swollen basally, less so distally, and with long, stiff, inclined or suberect pubescence, sparser than that on the club and arranged in somewhat irregular whorls (Fig. 1).

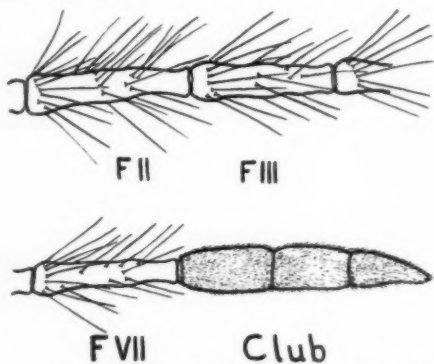


FIG. 1. Sections of typical male antenna of the genus *Pulvilligera*.

*Female:* Antenna with an indistinct three-segmented club, and all the funicular segments of about the same width.

#### *Pulvilligera maxima* Strand

*Male:* Length 13.0 mm.; abdomen 5.3 mm. Outline of head from above, oval, less than twice as thick as long, depressed on vertex and along an oblique line from each lateral ocellus to each compound eye, the vertex and most of the ocellar area with fine transverse rugulae which extend down over temples, the sculpture on the front sharper and more-or-less vertical, the occipital carinae sharp and evenly arcuate above; the ocellocapital line about twice as long as either the ocellocular or posterior ocellar line; scape compressed, evenly curved, and slightly longer than combined lengths of pedicel, ring segment, and FI; pedicel wider than FI; all funicular segments several times longer than thick, slightly decreasing in length progres-

sively from FI to and including FVII; club only a little shorter than combined lengths of FVI and FVII; antennal scrobe deep but not bounded by a distinct carina above. Pronotum a little longer than wide, sides nearly smooth, above with distinct transverse rugae, the emargination on anterior margin shallow; mesonotum to transverse line with prominent transverse rugae, those on the mesopraescutum more arcuate and sharpest, behind transverse line at most only weakly sculptured to smooth; basal segment of hind tarsus slightly longer than segments 2-5 combined. Propodeum with slight median longitudinal depression and crossed by numerous irregular rugae becoming more circular on either side of depression posteriorly; abdomen subdepressed.

Color mostly brownish to greenish-yellow with black (and brown) markings. Head brownish-yellow with front below antennal bases extending onto clypeus, along fronto-genal suture, gena below, the occiput bordering foramen magnum, three circular spots on vertex (one above each compound eye, another near the occipital carina), the area surrounding the ocelli and extending to compound eye and most of the antennal scrobe dark brown to black; most of scape and pedicel brownish-yellow, remainder of antenna black. Pronotum brownish-yellow (with shade of greenish-yellow) except below at sides and three separate longitudinal stripes above (two lateral, one median) which are black, the median weaker anteriorly; mesopraescutum and each mesoscutum with longitudinal median area dark brown, the remainder greenish-yellow; outer margin of axilla suffused with brown, the inner margin greenish-yellow; parapsidal furrow black; mesoscutellum greenish-yellow with a median longitudinal somewhat diamond-shaped black spot that extends to beyond the transverse line; prepectus and mesepisternum brown, remainder of pleura mostly brownish-yellow; median piece of metanotum greenish-

yellow; legs brownish-yellow except front coxa posteriorly and hind coxa anteriorly infuscated. Propodeum greenish to brownish-yellow except for the median depression, shallow groove below propodeal spiracle, and circular depression near posterior margin which are dark brown to black; tergum III (apparent first), except yellowish spot at side and sterna, black; each of terga IV-VI inclusive bordered posteriorly by narrow amber margin and with a circular lateral black spot above, otherwise these terga are predominantly reddish-brown above and light yellow at sides; tergum VII yellow except for narrow posterior amber margin.

Pubescence on body rather fine and sparse, black on antennae and dorsal areas of body and wings, remainder pale. Wings subhyaline; with fine, short, dense vestiture along whole anterior margin of costal cell of front wing; venation rather strong, proximal two-thirds of submarginal vein with 12-13 conspicuous bristles; stigmal vein short, stigma large, quadrate, the stigmal sector short, both surrounded with narrow infuscation (Fig. 2); venation dark brown or black.

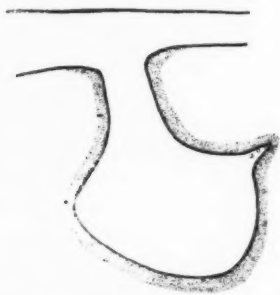


FIG. 2. Stigma of *P. maxima* male.

*Female*: Length 12.3 mm.; abdomen 5.5 mm. Ovipositor 31.5 mm. Structure of head and thorax, except for antennae and wings, much like that described for the male; scape compressed, slightly bent, about as long as pedicel, ring segment, FI, and one-half of FII combined; funicular segments subcylindrical,

decreasing slightly in length progressively in more distal segments, the proximal ones more than twice as long as thick. Propodeum only slightly depressed medially, sculptured with coarser more irregular rugae; abdomen compressed; ovipositor slender.

Head colored as in the male but less infuscated below and within antennal scrobe; antennae black except for the scape and pedicel, which are brown. Thorax colored as in the male but the median dorsal black stripe is more extensive and intensified, being weak or interrupted only on the anterior areas of both mesopraescutum and mesoscutellum; prepectus and mesepisternum lighter, and front and hind coxae without pronounced infuscation. Abdomen dark amber to brown except terga IV (apparent second) to VIII inclusive, each with yellow spot at side directed dorsad. Ovipositor sheath black.

Vestiture like that of male except proximal two-thirds of submarginal vein with about 14 conspicuous bristles, and dense vestiture present only on distal half of costal margin; wings subhyaline, venation strong, dark brown or black; stigma rather small (Fig. 3), somewhat oval, narrowly surrounded with infuscation; stigmal vein rather thick, about as long as greatest stigmal width, surrounded with narrow infuscation.

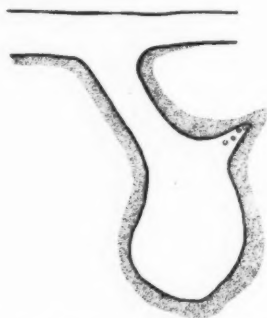


FIG. 3. Stigma of *P. maxima* female.

*Redescribed* from male, reared August 30, 1944, from *Pandanus* seed collected at mouth

of Evelyn River, Guadalcanal, August 23, 1944 (H. E. Milliron). Specimen in the collection of the U. S. National Museum.

**ALLOTYPE:** Female, with the same data as the male mentioned above except that it was reared August 25, 1944. Specimen in the collection of the U. S. National Museum.

**TYPE:** One of six males, probably in the Zoological Museum, Berlin, Germany. Type not examined.

**TYPE LOCALITY:** Taihanroku, Formosa.

**HOST:** Seeds of *Pandanus upoluensis* Martelli. (In the Solomon Islands.)

**DISTRIBUTION:** Formosa and Guadalcanal.

**ADDITIONAL SPECIMENS EXAMINED:** The writer also has studied a series of 86 males and 83 females, Mouth of the Evelyn River, Guadalcanal, 23 Aug. 1944, (H. E. Milliron). Ex seed of *Pandanus*. These are a part of the same lot as the above male and allotype female, and all were reared between August 23 and September 9, 1944. The *Pandanus* was later identified as *P. upoluensis*. The entire series is contained in the collection of the U. S. National Museum, 50 being preserved in alcohol.

**VARIATIONS:** *Male:* The lightest specimens are predominantly brownish- (and greenish-) yellow with reddish-brown over most of abdominal terga IV-VI inclusive, the black markings being reduced on the head to the area surrounding the ocelli and along a narrow line from the lateral ocellus to the compound eye, as well as narrowly around the foramen magnum. There is only a faint indication of the lateral spot above the eye (of the three spots on the vertex and temples). The three longitudinal stripes on the dorsum of the pronotum are reduced to separate elongate spots posteriorly, the median one being the faintest. Only an elongate black spot appears on the mesonotum, the remainder showing only faint traces of longitudinal black stripes. The propodeum is without trace of infuscation. The basal abdominal tergum (III) is blackish only at the base, and terga

IV-VI inclusive have only a slight indication of any black lateral spot above. All legs are yellowish.

The darkest male has pronounced black markings much as described but more intense and extensive. Most of the face below, except laterad of the clypeus and the area bordering the eyes in front, is very dark. The lateral spot above the eye is triangular, more enlarged, and extends down a considerable distance on the temples. The median spot extends posteriorly and unites with the black around the foramen magnum. A blackish extension appears on the front above, extending forward from the line described between the lateral ocellus and the compound eye. The lighter parts of the head are brownish to brownish-yellow. All lighter areas of the thorax are deeper than that described for the typical male, and there are three distinct dorsal longitudinal black stripes, the lateral one extending to the axilla and the median at least to the transverse line on the mesoscutellum (in some cases noticeably beyond), being only slightly interrupted at the anterior margin of the mesoscutellum. The front and hind coxae are blackish and the exterior surface of the hind femur is infuscated. The abdomen is much as described but the bands described as amber are black, and tergum VI is reddish-brown.

Between these two extremes all color gradations occur, but structurally there seems to be little variation. Larger, more robust males may be found with more distinct "verticillate" antennae and a few more conspicuous bristles on the proximal two-thirds of the submarginal vein (14-15). Males vary in size as follows: length 8.8-13.7 mm.; abdomen 3.8-5.3 mm.

*Female:* Females vary in color as do the males. The palest specimen is predominantly brownish- (or greenish-) yellow with black markings reduced on the head to the area around the ocelli and three spots on the vertex, with very little infuscation elsewhere.

The pronotum has the three separated longitudinal dorsal stripes which are weakest anteriorly. The continuation of these over the remainder of the thoracic dorsum is indicated by faint infuscation on the mesopraescutum and mesoscutum, while the mesoscutellum has a median, elongate oval blackish spot. All the legs are yellow. Only traces of infuscations are found on the propodeum and at the extreme base of the abdomen.

The darkest female has the color as described for the typical female but the scape and pedicel are dark brown to black. As with dark males, on some the black extends down onto the front from the line between the lateral ocellus and the compound eye. The lateral spot of the three on the head above is narrowly oval and on some it is extended as described for dark males. The median spot extends to unite with the black around the foramen magnum. The three black stripes on the dorsum of the thorax are very prominent and contrast with the adjacent greenish-yellow. The lateral stripe widens over the mesoscutum, becomes narrow posteriorly, and extends onto the axilla. The median stripe, which is abruptly broader at the anterior area of the mesopraescutum, becomes narrowed at the anterior margin of the mesoscutellum and extends considerably beyond the transverse line (on one specimen it extends almost the whole length). The coxae and femora and front tibia are infuscated, appearing for the most part dark brown or black. The propodeum is nearly entirely dark brown to black, and the abdomen, except for lateral yellow spots on terga IV-VIII as described, is also black.

Females vary in size as follows: length 10.0 (8 in curved position)-14.0 mm.; abdomen 4.4-6.6 mm.; ovipositor 24.0-33.0 mm.

COMMENTS: Specimens of this very variable species were all reared from seeds taken from the same *Pandanus* tree, which grew on the shore. The species is unusual in that it represents the largest species of Megastigmini

yet described. It probably occurs over most of the southwest Pacific. Females may be distinguished from those of the following new species by the more robust form, longer ovipositor, difference in appearance of the stigma, and several other characters.

*Pulvilligera neo-caledonica* n. sp.

*Female:* Length 9.5 mm.; abdomen 4.0 mm. Ovipositor 16.5 mm. Outline of head from above nearly circular but wider than long; vertex medially nearly flat, sublaterally somewhat depressed and with few shallow setigerous punctures; occipital carina sharp but not strongly developed, evenly arched except medially above; posterior ocellar line about equal to ocellocular line and both about two-thirds as long as ocelloccipital line; antennal scrobe only moderately deep and not compressed, not markedly bent, and equal to combined lengths of pedicel, ring segment, FI, and about one-fourth FII; pedicel oval, only a little wider than funicular segments, which become slightly shorter progressively from FI-FVII inclusive, and are nearly cylindrical and at least 2.5 to 3 times longer than thick; sculpture below and laterad of antennal bases strongest, consisting of irregular arcuate rugulae directed more or less obliquely from the margin of the clypeus; dorsal area of front adjacent to eye extensively reticulate, and less so below anterior to fronto-genal suture; vertex and temples weakly sculptured at most. Pronotum a little longer than wide, broadly arcuate anteriorly and with only a shallow median emargination, traversed above by regular rugulae only moderately strong; remainder of thoracic dorsum similarly sculptured except that the axilla and mesoscutellum are less noticeably rugulose to nearly smooth, especially nearly the entire surface of the latter, which shows no evidence of any external transverse line; first segment of metatarsus equal to or slightly longer than combined lengths of segments 2-4 inclusive. Propodeum somewhat ele-

vated, with irregular carinae originating along anterior margin and directed posterolaterally, median ones strongest and forming an inverted V with arcuate sides, the posterior surface less strongly sculptured with transverse arcuate carinae; abdomen compressed, smooth and polished; ovipositor sheaths slender.

Color, brown and black. Head brown, darker above, over vertex, temple, and occiput; antenna black, scape and pedicel dark brown; thorax brown, with median longitudinal stripe darker (concolorous with abdomen) and a dorso-lateral lighter and less distinct longitudinal stripe most prominent over pronotum; legs brown, the middle pair somewhat lighter. Propodeum and abdomen uniformly dark brown; ovipositor sheath black.

Vestiture mostly dark brown to black; some hairs on antenna suberect to erect, and those on thorax and abdomen somewhat longer and finer; wings nearly hyaline; venation brown, approximate distal third of costal cell of front wing with short vestiture, denser and more noticeable anteriorly along margin; proximal two-thirds of submarginal vein with 14 or 15 conspicuous bristles; stigma rather small, oval, directed toward outer wing mar-

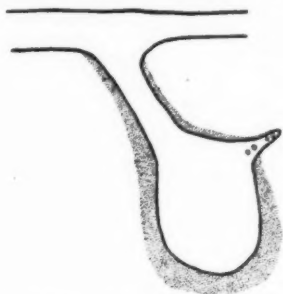


FIG. 4. Stigma of *P. neo-caledonica* female.

gin and surrounded by a narrow infuscation (Fig. 4), stigmal vein about as long as stigmal width.

*Male*: Length 9.5 mm.; abdomen 4.2 mm. Head similar to that of female, apparently

more sharply sculptured above; scape somewhat wider and more strongly curved; pedicel oval, much narrower than scape but distinctly wider than FI; all funicular segments long and slender, each not as markedly enlarged basally (and apically), with apparently somewhat fewer hairs (than in *P. maxima*); form of thorax and propodeum similar to that of female though somewhat more sharply sculptured, and the mesoscutellum appears weakly longitudinally striate; basal segment of metatarsus slightly shorter than combined lengths of segments 2-4. Abdomen subdepressed with tergum III (apparent first), smooth, the others finely aciculate.

Color similar to that of female except the scape is brownish-yellow and the remainder of the antenna black; abdominal tergum III dark brown; sterna, and remaining terga except amber posterior margin, are lighter brown.

Body pubescence similar to that of female. Denser vestiture on anterior margin of the costal cell of the front wing does not extend quite to base of cell; proximal two-thirds of the submarginal vein with about 15 conspicuous bristles; stigmal vein very short, the somewhat quadrate stigma sessile, both bordered by an infuscated area which is most extensive below the stigma (Fig. 5).



FIG. 5. Stigma of *P. neo-caledonica* male.

**TYPES:** Holotype, female, six miles east of Poindimie, New Caledonia, May 12, 1945 (H. E. Milliron). Ex *Pandanus* seed, May 20, 1945. U. S. National Museum catalogue



number 59289. Allotype, male, two paratype females, and a paratype male with the same data. All specimens are deposited in the collection of the U. S. National Museum, where is located another male (in rather poor condition, lacking both antennae beyond the pedicel) collected in Suva, Fiji, July 22, 1943, by R. A. Lever.

TYPE LOCALITY: Poindimie, New Caledonia.

HOST: *Pandanus tectorius* var. *neo-caledonicus* Martelli.

KNOWN DISTRIBUTION: New Caledonia, Fiji.

VARIATIONS: It is impossible, with so few specimens, to discuss fully the range of variation that exists in this species. Both structural and color differences are noted among the specimens at hand. The female may be slightly larger or noticeably smaller than the type, and the propodeum may be more coarsely and more irregularly sculptured. One paratype female is a little darker and the other considerably lighter, but in general the same pattern is manifested in all three females. The paratype male is slightly smaller and is paler over the lighter body regions, approaching a brownish-yellow (to somewhat greenish-yellow laterally on the mesoscutellum). The male from Fiji, aside from being considerably larger (length 11.0 mm.; abdomen 5.0 mm.), resembles the paler paratype.

COMMENTS: The specific and varietal name of the plant host, which was identified subsequently, does not appear on the labels. Although the basic thoracic color pattern of this species resembles that shown by *P. maxima* the two species are distinctly different. The shape of the stigma, weaker body sculpture, shorter basal segment of the metatarsus, and less extensive dense vestiture in the costal cell of the front wing, as well as the absence of three distinct spots on the dorsal region of the head, will serve to distinguish both sexes of this from *P. maxima*. In

addition, the females of *P. neo-caledonica* lack any distinct yellow pattern on the abdomen.

*Pulvilligera solomonensis* n. sp.

*Female:* Length 8.0 mm.; abdomen 3.5 mm. Ovipositor 17.0 mm. Outline of head from above broadly oval, about one-third wider than long; vertex nearly flat, traversed with fine rugulae barely attaining temples above; antennal scrobe moderately deep but not defined by sharp carinae dorsally; front with fine vertical rugulae which at the side converge toward the clypeus; gena and temple mostly smooth; posterior ocellar line about equal to the ocellocapital line and one-third longer than the ocellular line; occipital carina only moderately sharp, evenly arcuate above; scape more compressed beneath (or anteriorly) and only weakly bent; pedicel elongate oval, wider than FI and about one-half as long; funicular segments cylindrical, the proximal ones being more than twice as long as thick, the distal ones (FVI and FVII) about twice as long as wide. Pronotum about as long as its greatest width, the sides slightly arcuate in outline, the dorsal area with transverse rather regular rugulae, the side nearly smooth; mesopraescutum and mesoscutum similarly sculptured, the rugulae on the anterior area of the former being more arcuate and little sharper, behind less regular and more striate; axilla with more-or-less longitudinal striations; mesoscutellum without distinct sculpture (except anteriorly), posterior half nearly smooth; basal segment of metatarsus the longest but shorter than combined lengths of remaining segments. Propodeum with short irregular carinae anteriorly, the transverse median area with prominent arcuate carina, less distinctly sculptured behind; abdomen compressed; ovipositor sheaths slender.

Color reddish-amber or brownish-orange. Head mostly brownish or dark brownish-orange, the scape and pedicel brown, remainder of antenna black. Body and legs (the

latter though somewhat paler) brownish-orange, except pale median longitudinal infuscation on mesopraescutum and mesoscutellum; base of abdomen with little brown, and somewhat deeper amber distally above, otherwise abdomen is concolorous with thorax; ovipositor sheath black.

Vestiture throughout rather sparse and fine, that on head, body above, antenna, and ovipositor sheath black, elsewhere mostly pale. Wing subhyaline, its vestiture along the anterior margin of costal cell restricted to distal half; venation brown to dark brown; stigma rather small, more-or-less oval, and narrowly surrounded by infuscation (Fig. 6), the stigmal vein about as long as the greatest stigmal width.

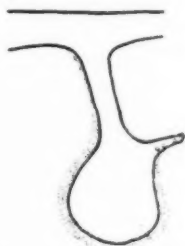


FIG. 6. Stigma of *P. solomonensis* female.

**Male:** Length 7.5 mm.; abdomen 3.5 mm. Form of head like that of the female; scape distinctly the widest segment of the antenna, compressed, and evenly curved; pedicel little wider than the base of FI; funicular segments all several times longer than wide, FI about equal to FVI, shorter than FII-V inclusive but longer than FVII, each noticeably swollen at the base but less so distally, the pubescence not dense and appearing less "verticillate" than in *P. maxima*. Sculpture of thorax and propodeum similar to that of female, the basal segments of the metatarsus distinctly shorter than the combined lengths of segments 2-5 inclusive. Abdomen depressed; tergum III (apparent first) smooth, those beyond very finely aciculate.

Color brownish-yellow and dark brown to

black. Coloration of head similar to that of the female; scape and pedicel brown, the former somewhat paler basally; remainder of antenna black. Thorax and legs brownish-yellow (or brownish-orange), dorsally with three rather distinct longitudinal brownish stripes, the median one extending over pronotum, mesopraescutum, and mesoscutellum approximately to the transverse line, and two dorso-lateral ones each extending over the pronotum and mesoscutum. Propodeum with some brownish color across the median area; abdomen dark brown to black above, median terga laterally and the sterna brownish-yellow.

Vestiture similar to that of female. Wing subhyaline, with dark brown to black venation; proximal two-thirds of submarginal vein with about 17-18 conspicuous bristles; dense vestiture along anterior margin of costal cell of front wing not extending quite to base of cell; stigma broadly oval (to subquadrate), nearly sessile, and surrounded by distinct infuscated area (Fig. 7).

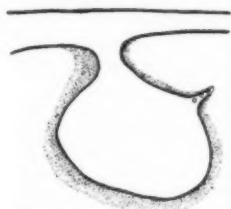


FIG. 7. Stigma of *P. solomonensis* male.

**TYPES:** Holotype, female, six miles from mouth of Tenaru River, Guadalcanal, August 13, 1944 (H. E. Milliron). Ex seed of *Pandanus*, reared August 14, 1944. U. S. National Museum catalogue number 59290. Allotype, male, with the same data. Paratypes: 44 females and 24 males, with same data as the type, all reared between August 14-25, 1944. All of these are deposited in the collection of the U. S. National Museum, as are 38 females and 6 males in alcohol, with the same data as the type except that these were reared on August 15, 1944.

TYPE LOCALITY: Mouth of Tenaru River, Guadalcanal, Solomon Islands.

HOST: *Pandanus* sp.

VARIATIONS: No significant variation in structure or color is noted among the series of females studied. Females which tend to be darkest show a pattern of brownish longitudinal stripes on the dorsum of the thorax very much like that described for the male, the median stripe being the stronger and especially conspicuous over the mesopraescutum and mesoscutellum to about the transverse line. Moreover, on such specimens usually the distal abdominal terga are darker brownish medially.

Except that the abdomen may be only subdepressed (and with some appearing as if petiolate) and the stigma may sometimes be more nearly circular, males of this species do not appear to vary significantly in structure. They do, however, show a marked range in coloration. Dark males are predominantly dark brown or black except that two dorso-lateral spots on the posterior margin of the pronotum, the inner angles of the mesoscutum and axilla, the extreme sides of the mesoscutellum, and the legs beyond the coxae are brownish-yellow. Several specimens of males lighter than these, but still darker than that described, have the anterior area of the pronotum entirely dark brown to black because of convergence of the longitudinal stripes, which are very prominent over the remainder of the thorax. The yellow on the thorax may vary from brownish-orange (or amber) to brownish-yellow.

COMMENTS: In coloration females of this species superficially resemble the North American *Megastigmus spermotrophus* Wach. All the material studied was reared from seeds taken from the same *Pandanus* tree. This species of host grows a considerable distance from the coast as isolated trees at the bottom of deep jungle ravines, and their ripe brilliant red fruit is seldom seen from the level of the jungle floor. The drupes are

similar to those of *P. motleyanus* Solms-Laub.

Females of this species may be distinguished from those of the preceding species by their distinctive color and by the shape of the stigma. Males may be recognized by the short stigmal vein, the appearance of the stigma, and by the usually depressed character of the abdomen.

#### NOTE

*P. gigantea* Gir. was described in 1928 from a female and a male taken at Townsville, Australia. It is possible that Girault's *Epimegastigmus titanus* (and *E. giganteus* referred to and compared in the description published in 1939) may belong to *Pulvilligera*. Inasmuch as no material of these species was available for study, the matter of their classification must remain unchecked temporarily.

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# Inter-tidal Ecology at Narrow Neck Reef, New Zealand (Studies in Inter-tidal Zonation 3.)<sup>1</sup>

VIVIENNE DELLOW<sup>2</sup>

## INTRODUCTION

THE PLANT and attached animal communities at Narrow Neck Reef, Auckland, have been studied in relation to factors that may be concerned with determining their vertical zonation. Observations were made between January, 1947, and July, 1948.

Certain levels on the shore appear to be more critical than others in determining the upper and lower limits of species and of communities; these levels may coincide with heights above low water at which there is a sudden change in environmental conditions. In accordance with the general aim of this series, an investigation has been made into the number and position of levels which may be critical at Narrow Neck.

*Acknowledgments:* The writer wishes to express her sincere appreciation to Professor V. J. Chapman for assistance and helpful criticism throughout this work; to Dr. G. F. Papenfuss and to Miss L. B. Moore for advice on the text; to Mr. V. W. Lindauer for assisting with the identification of Phaeophyceae and Rhodophyceae; to Mr. J. E. Morton for identification of the animals; and to Mr. L. Finch for help with the compilation of the map.

## TERMINOLOGY

While it is not proposed to enter into a lengthy discussion on the controversial topic

of marine ecological terminology, it does appear essential to state precisely the sense in which each term is employed. However, it seems unreasonable to me either to give new meanings to words now in current use in ecological nomenclature, or to impose a new series of technical terms on an already overburdened vocabulary.

As the word "littoral" has been used in so many different ways, I prefer to call that part of the shore between extreme high water mark of spring tides and extreme low water mark of spring tides the "inter-tidal region," where these extreme levels are the means of monthly extremes for the locality over a number of years. The area between Mean Extreme Low Water Spring Tide and Extraordinary Low Water Spring Tide (= Auckland Harbour Board Datum) corresponds to Stephenson's sublittoral fringe. Below this is the sublittoral or subtidal region, which is never exposed by the tide. That part of the shore from above Extreme High Water Spring Tide to the upper limit of wind-borne spray is regarded as the supralittoral, or supratidal region. It includes the somewhat arbitrary "splash" and "spray" zones, neither of which is of much importance at Narrow Neck.

Within the inter-tidal region exists a number of marine biotic communities. Some authors consider that these should be treated as though they were equivalent to terrestrial climax communities. In general, however, the marine units occupy smaller areas and may be much less long-lived, owing to the shorter life-history of the component organisms and to the super-position of the tidal factor on the climatic complex. On the other hand, because of this relative impermanence

<sup>1</sup>This paper forms part of a thesis presented for a Master of Arts degree at Auckland University College (University of New Zealand) in October, 1948. An abridged version was read before the Botany Division of the Seventh Pacific Science Congress at Auckland, in February, 1949.

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as compared with, for example, forest vegetation, it could be maintained that the units do not justify the ecological status of a climax. In this paper, support is given to the former view; for there does appear to be a certain, fairly constant sequence of events which may be in the nature of a true succession leading up to a relatively stable climax condition. Nevertheless, more detailed work will be necessary for a satisfactory elucidation of this problem.

In assessing the ecological importance of animals in a community, one of three views may be adopted: (1) that animals are biotic factors external to the plant community; (2) that animal communities exist where plants form part of the habitat; (3) that plants and animals are interrelated, co-acting constituents of an integrated biotic community (Phillips, 1931). The third view is adopted by several authors, including Clements and Shelford (1939), who propose the biome or biotic formation as the basic unit on land or sea. The concept seems the most suitable one so far put forward for application to seashore communities and is adopted in the present work.

The broad vertical zonation in the Hauraki Gulf can be compared with that described by Stephenson (1939; 1944) for the coast of South Africa, and more recently by Dakin, Bennett, and Pope (1948) for the New South Wales coast. Four main zones can be distinguished here, of which characteristic dominants are: (1) *Melaraphe* (a littorinid species), (2) barnacles, (3) small, turf-forming algae, and (4) large, brown algae. Each zone is regarded as constituting a separate biome, or biotic formation, since these divisions appear to be real entities of world-wide occurrence. Using Stephenson's terminology, these are equivalent to: (1) littorina zone, (2) balanoid zone, (3) mixed algal zone, and (4) sublittoral fringe.

In this paper, terms used in connection with the ecology of higher plants have been

applied to units on the seashore, according to the following definitions:

*Biome*: a biotic community with the rank of a climax formation (Clements and Shelford, 1939).

*Association-complex*: a group of associations occurring in successive belts which follow one another in a regular, constantly recurring sequence (Cranwell and Moore, 1938).

*Association*: a climax community with two or more dominants (Clements, 1916).

*Consociation*: a climax community with a single dominant (Phillips, 1931).

*Fasciation*: a portion of an association in which one or more dominants have dropped out and have been replaced by other forms, the general aspect of the community remaining unchanged (Clements, 1936).

*Clan*: a small community of subordinate importance but of distinctive character, frequently the result of vegetative propagation (Clements, 1936).

*Aspect society*: A seasonal community characterized by one or more subdominants.

*Belt*: a continuous, horizontal strip of the coast occupied throughout most of its length by one association, which may be interrupted by another community, depending on slightly local conditions (Cranwell and Moore, 1938).

*Zone*: the horizontal sector occupied by one formation and characterized by dominants of one or more associations.

#### PHYSICAL FACTORS

Narrow Neck lies about 2 miles north of Devonport, on the north shore of Waitemata Harbour, Auckland. The Harbour constitutes a ramifying arm of the Hauraki Gulf, which is almost landlocked and protected from the full force of onshore gales from the Pacific Ocean by Great Barrier and Little Barrier Islands to the north and by Coromandel Peninsula to the east. The reef itself forms part of a submarine shelf extending seawards to the Rangitoto Channel, the greatest depth of



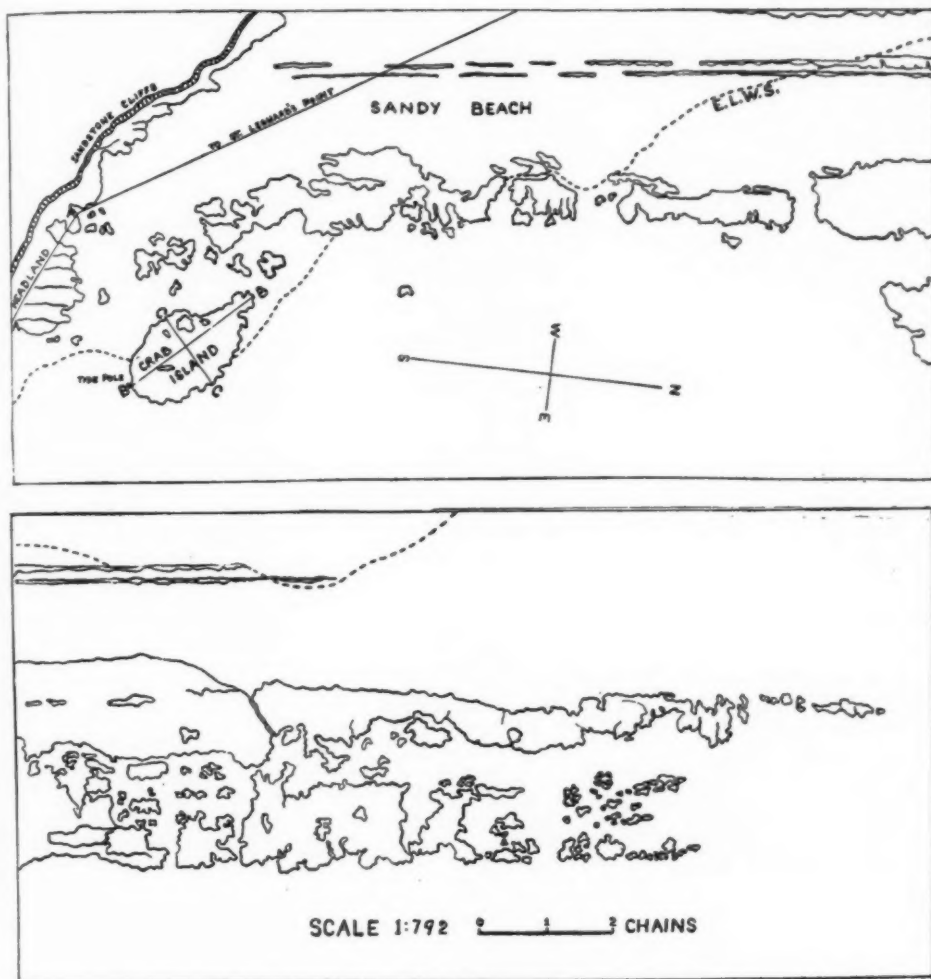


FIG. 1. Map of Narrow Neck Reef, showing position of Traverses A, B, and C. Traverse A, on Headland, top left; Traverses B and C, on Crab Island.

water at any point surrounding the reef being 2.5 fathoms. A thin layer of fine silt and mud is deposited on the gently inclined, exposed rock surface in calm weather.

There are two drainage outlets in the vicinity: one at the southern end of Narrow Neck Beach, the other at St. Leonard's Point. A considerable increase in both turbidity of water and abundance of colonial diatoms is

apparent about these places. The area studied most intensively extends from the northern end of Narrow Neck Beach to St. Leonard's Point, a distance of about five-eighths of a mile.

The reef is made up of three main groups of rock which have been named the Headland, Crab Island, and the Main Reef (see map, Fig. 1). The Headland at the cliff base

is barely covered by an extreme high spring tide. Crab Island (so-called because of the abundance of the large shore crab, *Leptograpsus variegatus*) is a small island of rock which, although slightly more elevated than the Main Reef, is covered by even the lowest high tides. At no point is the Main Reef higher than M.S.L. (6.22 feet above Auckland Harbour Board Datum).

The rock is a heterogeneous, fine, volcanic agglomerate, locally known as Parnell Grit (Bartrum and Turner, 1928). This is conformably interbedded with Waitemata Sandstone, which forms the major part of the Auckland Isthmus. There are a large number of irregular joints in the rock, along which deposition of brittle iron compounds has taken place.

The Auckland district has a maritime climate, with a relatively small daily and annual variation in temperature and precipitation (Beveridge and Chapman, 1950). Prevailing westerly winds are off-shore at Narrow Neck, and hence wave action is usually slight. Sea temperature closely follows that of the surrounding land.

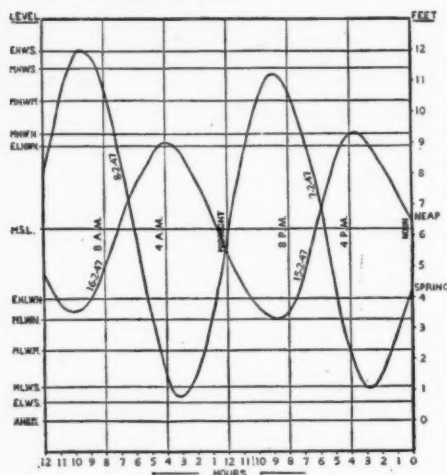


FIG. 2. Chart indicating extreme tidal ranges recorded over two 24-hour periods in the month of February, 1947, by the self-registering tide gauge at Queen's Wharf, Auckland.

There are no fresh-water outlets which would have a significant effect on the salinity of seawater in the locality. Isolated determinations were made by Hounsell (1935) at North Head, 2 miles south of Narrow Neck, and at Rangitoto Beacon to the east, where the values were 35.00 and 35.10, respectively. Both samples were collected in the morning.

The pH of seawater at Narrow Neck lies between 8.0 and 8.1, the value remaining constant throughout the year (Ambler and Chapman, in press).

Tides in the Hauraki Gulf are semi-diurnal, with an extreme spring range of about 12 feet and an extreme neap range of about 5 feet. Day and night tides differ slightly in amplitude, the night tides being greater in summer and smaller in winter. Figure 2 shows typical extreme neap and spring tides recorded for the locality by the Auckland Harbour Board. It was found from readings on a tide pole at Narrow Neck that there is no significant disparity in time and rate of tidal rise and fall in comparison with the recordings on the self-registering tide gauge at Queen's Wharf.

Tide levels were averaged from Auckland Harbour Board marigrams for the years 1945, 1946, and 1947 in order to avoid using data for 1 year only. The method of calculating the levels was that used by Beveridge (in Beveridge and Chapman, 1950). There is no significant difference between the figures for 3 years presented in Table 1 and those of Beveridge and Chapman for the year 1945. Extreme figures in Table 1 are means of monthly extremes. All heights are expressed in feet above Auckland Harbour Board Datum (0.00 feet, or Extraordinary Low Water Spring Tide).

TABLE 1  
TIDAL DATA FOR AUCKLAND HARBOUR

TIDE LEVEL	HEIGHT IN FEET ABOVE A.H.B.D.
Extreme High Water Springs (E.H.W.S.)	11.95

Mean High Water Springs (M.H.W.S.)	11.41
Mean High Water Mark (M.H.W.M.)	10.35
Mean High Water Neaps (M.H.W.N.)	9.28
Extreme (Lowest) High Water Neaps (E. (L.) H.W.N.)	8.88
Mean Sea Level (M.S.L.)	6.22
Extreme (Highest) Low Water Neaps (E. (H.) L.W.N.)	3.96
Mean Low Water Neaps (M.L.W.N.)	3.29
Mean Low Water Mark (M.L.W.M.)	2.29
Mean Low Water Springs (M.L.W.S.)	1.12
Extreme Low Water Springs (E.L.W.S.)	0.60
Auckland Harbour Board Datum (A.H.B.D.)	0.00

LEVELING SURVEY

To obtain quantitative data concerning the levels and vertical range of the more important littoral plants and animals, a series of traverses was made in different parts of the area (see Figs. 1 and 3-6). In each case, the leveling staff was placed as near as possible to the average limit of the vertical range of the species. Elevation or depression levels due to local modifications were not taken into account. Levels of species such as *Caulerpa sedoides* and *Splachnidium rugosum* which did not occur across the paths of the traverses were obtained as isolated spot-heights from elsewhere within the area. The traverses were

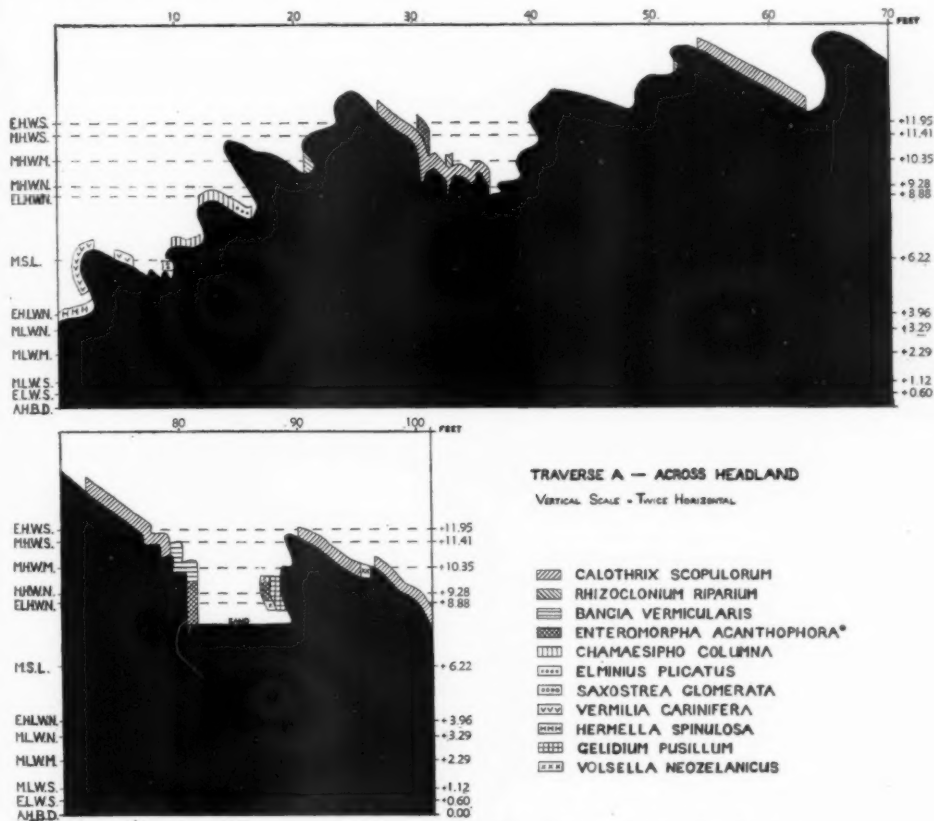


FIG. 3. Traverse A. (\* Found to be *Enteromorpha procerata* f. *minuta*.)

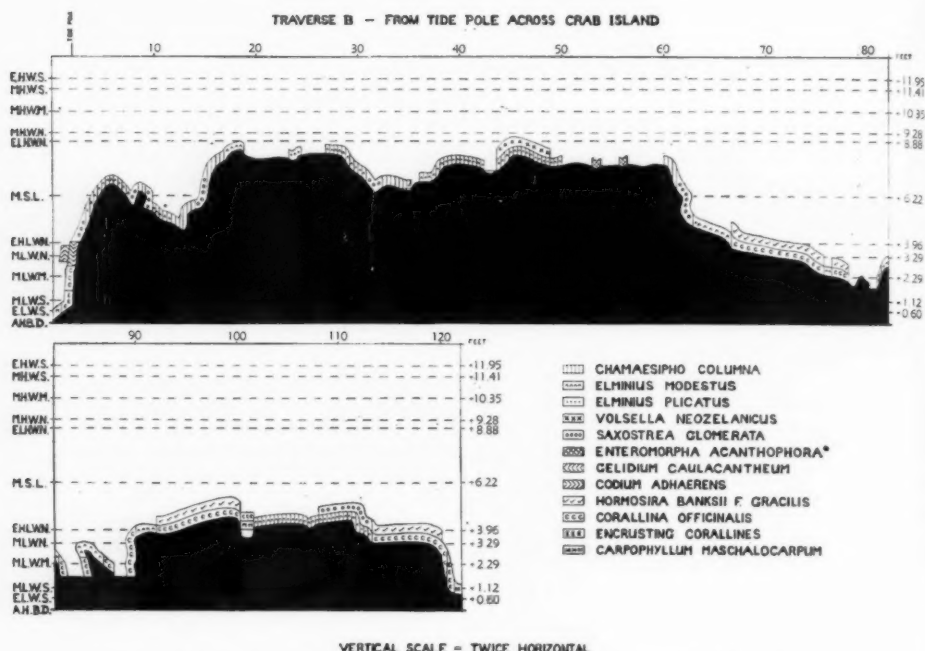


FIG. 4. Traverse B. (\* Found to be *Enteromorpha procera* f. *minuta*.)

mapped in late summer (January–February, 1948) and therefore include summer aspect societies.

*Traverse A* (Figs. 1, 3): Across Headland; length 101 feet; bearing  $116^{\circ} 20'$ .

This traverse was designed to illustrate typical zonation of the communities at higher levels. It passes from M.L.W.N.<sup>3</sup> to above E.H.W.S. and crosses in front of a small cave. The angle of dip of the rock, which is to the north, is clearly indicated. Dip faces of the inclined ledges are exposed to maximum insolation, while strike faces are shaded for most of the day. The different aspects show differences in the species colonizing the same level: for instance, near the end of the traverse, *Gelidium pusillum* and *Volsella neozelanicus* flourish on a shaded, vertical strike face at the same level as *Calothrix scopu-*

*lorum*, which usually grows above them.

In front of the cave mouth (between 80 and 90 feet) the sand level limits the downward colonization of *Enteromorpha procera* f. *minuta*.

*Traverse B* (Figs. 1, 4): Crab Island, from the tide pole across the longer axis of the island; length 122 feet; bearing  $136^{\circ} 30'$ .

In *Traverse B* the relative positions above A.H.B. Datum of the more important communities below E.(L).H.W.N. can be seen. The traverse starts at A.H.B.D., at which level *Carpophyllum maschalocarpum* is flourishing, and passes upwards successively through encrusting corallines, *Corallina officinalis*, *Gelidium caulacanthum*, oysters, and barnacles. It illustrates the wide extent of both the balanoid community at higher levels and of *Corallina* and *Hormosira* lower down on flat surfaces. The steeply ascending rock slope at the beginning of the traverse is shaded for

<sup>3</sup>See Table 1 for full explanation of abbreviations used throughout this paper.

most of the day and has a southwesterly aspect. *Codium adhaerens* flourishes here while *Hormosira* is absent. Telescoping of belts with increasing angle of slope is evident.

**Traverse C** (Figs. 1, 5): Crab Island, across the shorter axis, at right angles to Traverse B; length 70 feet; bearing  $46^{\circ} 40'$ .

Traverse C shows Crab Island in profile from the shore to the seaward face of the island. The change in nature and in specific composition of communities with change in level is very similar to that in Traverse B. *Enteromorpha procera* f. *minuta* and *Elminius plicatus* are poorly developed on Crab Island. It will be observed that the encrusting coralline belt descends lower than usual to seaward. *Corallina* and *Hormosira* are growing just below the 8-foot level, 4 feet above their normal upper limit, under pool conditions.

**Traverse D** (Figs. 6a, b): St. Leonard's Point; length 269 feet; bearing  $45^{\circ}$ .

Traverse D, the longest, runs in a direct line from high to low water. It is not shown on the map of the reef because the shape of the area as a whole is too awkward to allow the inclusion of St. Leonard's Point on a map of that scale.

The strata of the cliffs above the point are not tilted as they are at the Headland. The dip and strike of the ledges below form a correspondingly regular sequence from the cliff base to the seaward end of the point. Much of the intervening rock is flat and is covered with thick deposits of mud. The water about the point is always turbid with much suspended matter from the sewage outflow. The general zonation, however, is remarkably similar to that obtaining at Narrow Neck.

*Melaraphe oliveri* and *Calothrix scopulorum* are widespread between M.H.W.S. and E.H.W.S. Beneath the overhanging ledge 36 feet from the start of the traverse, *Ralf-*

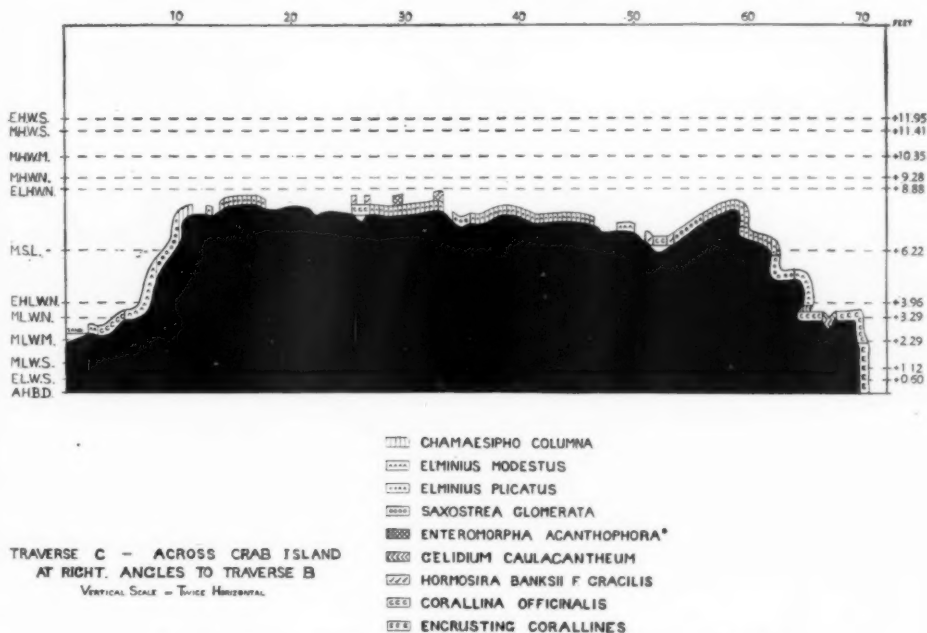


FIG. 5. Traverse C. (\* Found to be *Enteromorpha procera* f. *minuta*.)



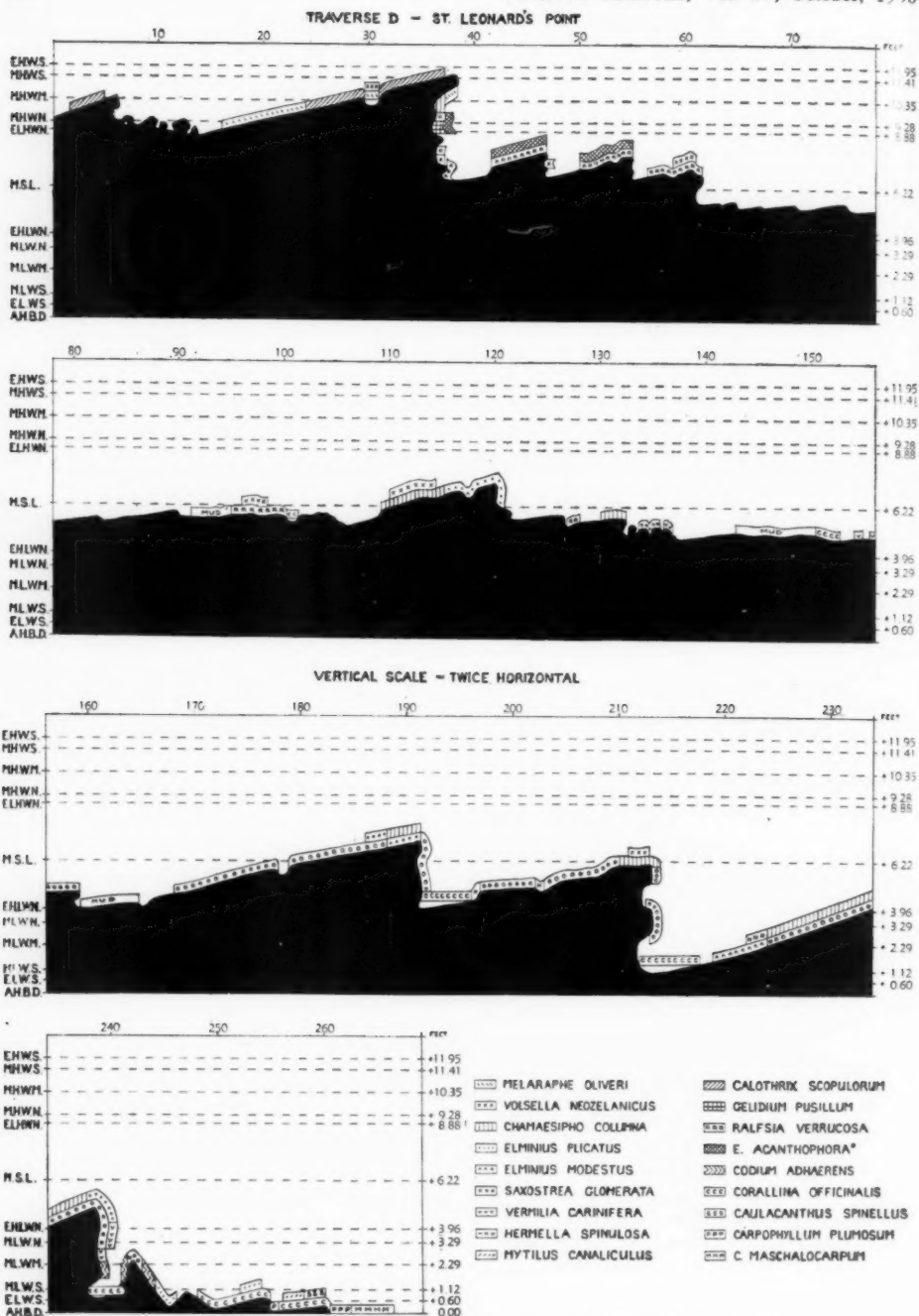


FIG. 6. Traverse D. (\* Found to be *Enteromorpha procera* f. *minuta*.)

*sia verrucosa* and *Enteromorpha procera* f. *minuta* are growing above their normal level. Together with *Volzella neozelanicus* they colonize wide stretches of the relatively flat rock about M.S.L. Slight elevations are marked by a local increase in abundance of the large barnacle *Elminius plicatus*. The chief difference between St. Leonard's Point and Narrow Neck Reef lies in the presence of the *Mytilus*—Attached Algae Community at the former locality about E.L.W.S. (see p. 370).

From data obtained in the leveling survey, Figure 7 was constructed by plotting the vertical ranges of 25 of the more important plants and animals against the curve for the percentage of annual exposure at each level. The average amount of exposure and submergence endured by each species can therefore be calculated from this chart. (Each limit represents the average of several readings on the leveling staff.)

#### BIOTIC COMMUNITIES

These are described roughly in their order of occurrence from high to low water. It should be observed, however, that the upper limit of one association may overlap the lower limit of the one immediately above: for example, the lower limit of the *Corallina*—*Hormosira* association is given as 0.8 feet, while the upper limit of the Encrusting Coraline association is 1.7 feet. This may be explained by local differences in such factors as topography and exposure to wave action which tend to allow the replacement of one community by another. Thus, a horizontal as well as a vertical sequence with changed conditions of habitat may be distinguished. The range of exposure undergone by each community is expressed as a percentage of the total possible exposure per annum.

#### *Littorina* Formation

##### 1. *Calothrix*—*Melaraphe* Association

Vertical range: 12.9–9.2 feet. Between E.H.W.S. and M.H.W.N.

Exposure: 100–78 per cent.

*Calothrix scopulorum* (d)<sup>4</sup>  
*Rhizoclonium riparium* (ld)  
*Enteromorpha procera* f. *minuta* (f)  
*Microcoleus acutissimus* (o)  
*Melaraphe oliveri* (d)  
*Lyngbya lutea* (a)  
*Lophosiphonia macra* (lf)  
*Monostroma latissimum* (r)

Two separate consociations are recognizable:

##### a. *Calothrix* Consociation

The dull, blackish-green crusts of *Calothrix scopulorum* cover extensive areas of exposed rock about the highest levels of the intertidal region, especially on flat or gently sloping surfaces exposed to strong insolation. After a high spring tide or a heavy rain, the thick sheaths surrounding the trichomes become extremely gelatinous. *Calothrix* does not tolerate stagnation because in small, water-filled depressions, in which *Lophosiphonia macra* is often present, growth of *Calothrix* ceases abruptly. During periods of continuous exposure, the encrusting mat becomes dry and cracked and peels off easily. At such times the rock colonized by *Calothrix* may become white because of salt efflorescence. The upper limit of the consociation, which is much more clearly defined than the lower, is probably correlated with sudden extreme changes in salinity and microclimate. An example of sudden temperature changes in the *Calothrix* belt was recorded on February 8, 1948. At noon, rock temperature reached 33.3° C. After a brief shower it fell to 24° C.

##### b. *Melaraphe* Consociation

As *Calothrix* becomes sparser in the lower 2 feet of its vertical range, the small gastropod *Melaraphe oliveri* assumes dominance.

<sup>4</sup>d = dominant                      o = occasional  
 a = abundant                    l = local  
 f = frequent                      r = rare

The boundaries of this community cannot be delimited precisely in terms of tide levels since *Melaraphe* is able to move within a relatively restricted area to a more favorable

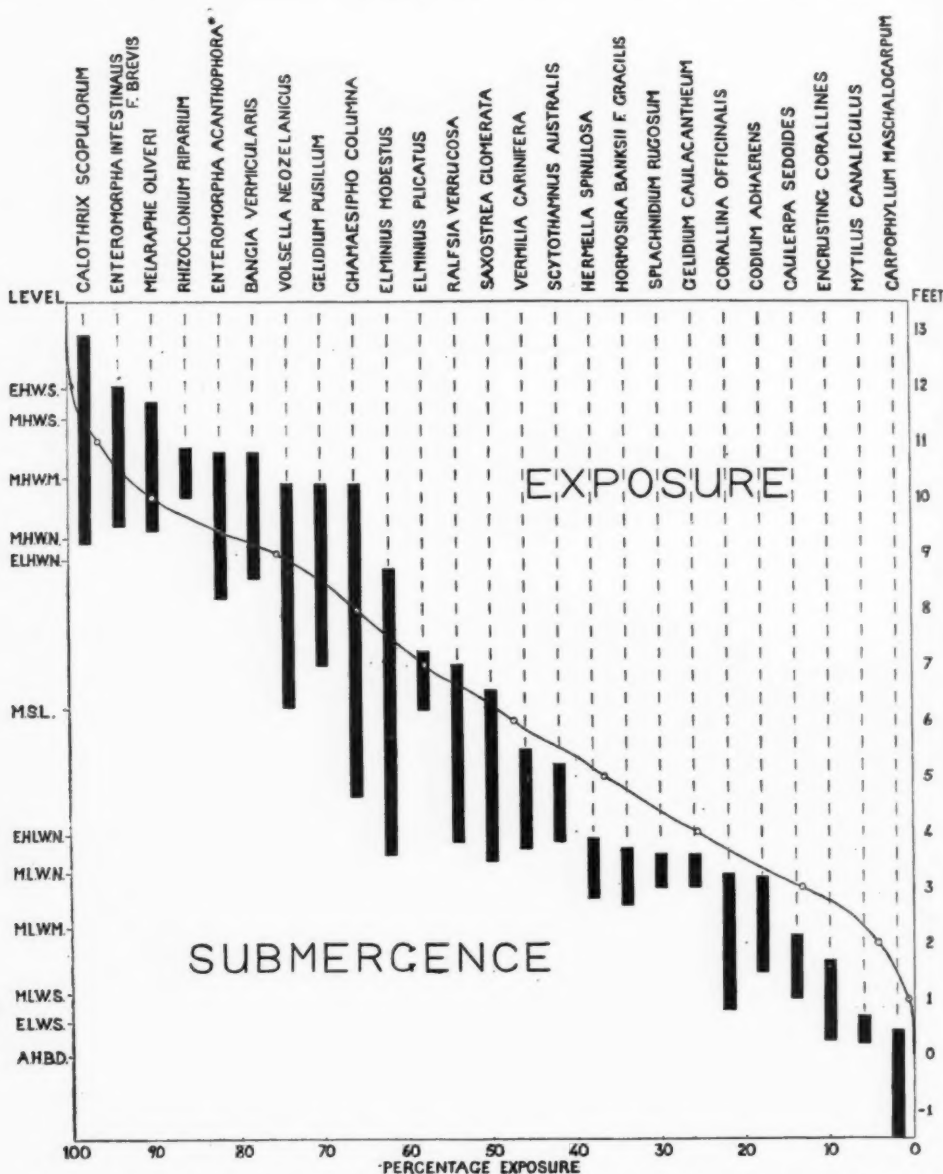


FIG. 7. The vertical range of 25 inter-tidal species (\* found to be *Enteromorpha procera* f. *minuta*) in relation to annual percentage exposure and submergence. (The limits are averaged from data obtained in the four traverses.)

local environment. During a hot summer afternoon, when the tide is low, it will migrate to a shallow pool beneath an overhanging ledge, while just after being uncovered by the tide it will present a more uniformly scattered pattern of distribution.

#### *Balanoid Formation*

### 2. *Enteromorpha* — *Gelidium* — *Volsella* (*Modiolus*) Association

Vertical range: 10.8–6.3 feet. Between M.H.W.M. and M.S.L.

Exposure: 94.7–58 per cent.

- Enteromorpha procera* f. *minuta* (d)
- Volsella* (*Modiolus*) *neozelanicus* (d)
- Cbamaesipho columna* (a)
- Onchidella patelloides* (o)
- Gelidium pusillum* (d)
- Ralfsia verrucosa* (a)
- Centroceras clavulatum* (f)
- Elminius modestus* (f)

Although sometimes epiphytic on *Geli-*

*dium pusillum*, *Enteromorpha procera* f. *minuta* more often dominates in exposed situations immediately below the *Calothrix*—*Melaraphe* association. The small mussel *Volsella* (*Modiolus*) *neozelanicus* is usually entangled within the dense cushions formed by *G. pusillum*. Striking evidence of the reactions of these species to exposure and shelter is seen on the rock face south of the Headland cave (Traverse A, Fig. 3). Where the slope is vertical, with a curve that faces the incoming tide, *Enteromorpha* dominates. Where the rock is shaded or overhanging, the dominants are *Volsella* and *Gelidium*.

#### a. *Enteromorpha* Consociation

*E. procera* f. *minuta* fluctuates seasonally in abundance. Although present all the year round, it reaches maximum extent in autumn and winter, with a secondary growth period in spring. During the hottest summer months (January and February) the *Enteromorpha* community on wharf piles in the Auckland



FIG. 8. *Volsella neozelanicus* consociation on a flat ledge between Narrow Neck and St. Leonard's Point.

Harbour is absent, though still growing at similar levels in the Narrow Neck locality. The mat formed by this species serves as a trap for sand and silt, which act as a moisture reservoir during periods of exposure by the tide.

b. *Volsella* Consociation (Fig. 8)

*Volsella neozelanicus* may be profoundly dominant below the level usually colonized by *Gelidium*. This suggests that the upper limit of *Volsella* is raised through association with the red alga, the thallus of which acts like a sponge in conserving moisture.

The barnacles *Chamaesipho columna* and *Elminius modestus* and the encrusting *Ralfsia verrucosa* are subordinate members of this community.

3. *Chamaesipho* — *Elminius* — *Saxostrea* Association (Fig. 11)

Vertical range: 10.2–3.6 feet. Between M.H.W.M. and M.L.W.N.

Exposure: 92–21.3 per cent.

- Chamaesipho columna* (d)
- Saxostrea glomerata* (d)
- Scytothamnus australis* (ld)
- Enteromorpha procera* f. *minuta* (a)
- Splachnidium rugosum* (f) (summer)
- Pylaiella novae-zelandiae* (f)
- Caulacanthus spinellus* (o)
- Gelidium caulacanthum* (o)
- Bangia vermicularis* (o) (winter)
- Elminius modestus* (d)
- Elminius plicatus* (ld)
- Ralfsia verrucosa* (ld)
- Volsella neozelanicus* (a)
- Sypharochiton pellis-serpentis* (f)
- Lepsiella scobina* (f)
- Cellana radians* (f)
- Cellana ornata* (o)
- Urospora penicillaeformis* (l)  
(autumn)

This association, which is included by Oliver (1923) in his "Shelled Animals Formation," has the widest range of distribution of any inter-tidal community in the region and

is subject to the greatest variety of changes in environmental conditions.

a. *Chamaesipho* Consociation

*Chamaesipho columna*, the smallest of the common inter-tidal barnacles, is usually to be found forming a greyish-white, horizontal belt about the mark of M.H.W.N. At this tide level the community is a closed one in places of optimum development, but towards its upper limit (M.H.W.M.) the individual barnacles are more scattered, and species from higher associations, e.g., *Volsella neozelanicus*, may become locally dominant.

b. *Elminius*—*Scytothamnus* Fasciation

*Elminius plicatus*, the largest of the inter-tidal barnacles in this locality, is locally dominant just above M.S.L., where it may form a closed community, usually not exceeding 1 foot in vertical extent. *Chamaesipho columna* and sometimes *Caulacanthus spinellus* are common epiphytes on *E. plicatus*. The dark brown fronds of *Scytothamnus australis* are the prevailing feature of portions of the community, co-dominating with either *E. plicatus* or *E. modestus*, the latter mainly at lower levels just above the coralline turf. During periods of emergence the exposed parts of the thalli become dry and parched, while portions lying directly upon the barnacles are still quite damp.

c. *Elminius modestus* Consociation

This community may be present at any level between M.S.L. and M.L.W.N. Perhaps the most striking ecological attribute of *E. modestus* is its ability to exist in muddy water. At Narrow Neck it flourishes on the gently sloping dip face of the main reef above *Coralina*, where at times there is a layer of fine silt and mud ½ inch thick. *E. modestus* is equally at home on flat, vertical, or sloping faces, whether shaded or exposed to sun, and on both upper and under sides of boulders. Once established, it can withstand relatively strong tidal currents and wave action. It is prevented from colonizing all the available rock surface within its vertical range by com-



petition, within narrower limits, from other animal communities, in particular those formed by the common rock oyster, *Saxostrea glomerata*, and by tubicolous polychaetes like *Hermella spinulosa* and *Vermilia carinifera*.

*Chamaesipho* and *E. modestus* owe their ubiquitous nature to their ability to reproduce in large numbers throughout the year (Moore, 1943) and to their wide tolerance with respect to their substrates.

#### d. *Saxostrea* Consociation (Fig. 9)

Vertical range: 6.5–3.5 feet. Between M.S.L. and M.L.W.N.

Exposure: 53–20 per cent.

*Saxostrea glomerata* occurs in a conspicuous belt, both upper and lower boundaries of which are sharply delimited. A species most consistent with regard to vertical range, *Saxostrea* shows relatively little variation in pattern of distribution in response to factors such as wave action, light incidence, and angle of slope of the substrate (Doty, 1946). The consociation usually gives way above

and below to a balanoid community. On the main reef, however, which is nowhere higher than 6 feet, the oyster forms the uppermost belt.

The few associated species are nearly all animals. The gastropod *Lepsiella scobina* causes much damage by boring holes with its radula through the shell of the oyster, which it extracts in pieces. Powell (1947) records that *Lepsiella* can pierce an oyster shell in 45 minutes.

#### 4. *Hermella*—*Vermilia* Association

Vertical range: 5.5–2.8 feet. From just below M.S.L. to just above M.L.W.M.

Exposure: 42–10 per cent.

- Hermella spinulosa* (d)
- Chamaesipho columna* (a)
- Codium adbaerens* (f)
- Gelidium caulacanthum* (o)
- Vermilia carinifera* (d)
- Elminius modestus* (a)
- Centroceras clavulatum* (o)



FIG. 9. *Saxostrea glomerata* consociation on a heavily eroded ledge near St. Leonard's Point.

*Lunella smaragda* (f)  
*Neobais baustum* (o)

An association dominated by the tubicolous polychaetes *Hermella spinulosa* and *Vermilia carinifera* is characteristic of the shaded (strike) faces of ledges on Narrow Neck Beach which are adjacent to sand. *Vermilia* nearly always occurs above *Hermella*, although the two species occasionally intermix. *Hermella* appears to be more tolerant of mud. At St. Leonard's Point it reaches maximum development, forming sandy hummocks which are easily eroded by wave action and which provide a place of refuge for numerous small crabs. *Vermilia carinifera* consists of calcareous tubes attached lengthwise to the substrate. The animal occupies only the opening of the tube and protrudes when lying in a small pool, but if the shell is exposed to air it retreats within the tube, which it closes with a shelly operculum.

Subordinate species include *Codium adbaerens*, forming compact, radiating cushions on either sandy or calcareous worm tubes (Fig. 10), together with the usual barnacles and molluscs, including chitons, limpets, *Lunella smaragda*, and occasionally *Neobais baustum*.

#### Lower Mixed Algal Formation

#### 5. *Corallina*—*Hormosira* Association (Fig. 11)

Vertical range: 3.7–0.8 feet. Between E.(H).L.W.N. and M.—E. L.W.S.

Exposure: 22.2–0.5 per cent.

*Corallina officinalis* (d)  
*Colpomenia sinuosa* (a)  
*Codium adbaerens* (f)  
*Caulacanthus spinellus* (f)  
*Laurencia botrychioides* (f) (summer)  
*Laurencia thyrsoifera* (o)  
*Dictyota ocellata* (o)  
*Derbesia novae-zelandiae* (r)  
*Polysiphonia* sp. (r)  
*Chamaesipho columna* (f)

*Tethya fissurata* (f)  
*Hormosira banksii* f. *gracilis* (d)  
*Leathesia difformis* (a)  
*Gelidium caulacanthum* (f)  
*Enteromorpha procera* f. *novae-zelandiae* (f)  
*Splachnidium rugosum* (f) (summer)  
*Microdictyon mutabilis* (o)  
*Symphyocladia marcbantioides* (o)  
*Dasya subtilis* (r)  
*Lophurella caespitosa* (r)  
*Elminius modestus* (f)  
*Lunella smaragda* (f)

Below the level of low water neap tides, there is an abrupt change in type of community: animals become of secondary ecological importance, and algae of one kind or another are physiognomic. There is also a notable increase in the number of species and, in general, a decrease in numbers of individuals. In the relatively sheltered waters of the Hauraki Gulf the *Corallina*—*Hormosira* association is the most widely distributed algal community in the inter-tidal region. Dull reddish-brown in gross appearance, it covers all the available space on flat or gently inclined rocks between low water neap and low water spring tide levels. Although *Hormosira banksii* often dominates a separate association in other localities (e.g., on Takapuna Reef), at Narrow Neck it is seldom found growing apart from *Corallina*. The regular line delimiting *C. officinalis* from the balanoid association above (Fig. 11) is broken here and there by upward penetration of the *Corallina*—*Hormosira* association along cracks in the rock which serve as drainage channels.

*Hormosira* seems unable to establish itself in large numbers on vertical or steep slopes. Towards the lower limit of the association it gradually drops out, and *Corallina* assumes dominance. The latter forms a short turf of tufted plants, apparently comparable to the algal turf described by Stephenson (1939, 1944) for South Africa.

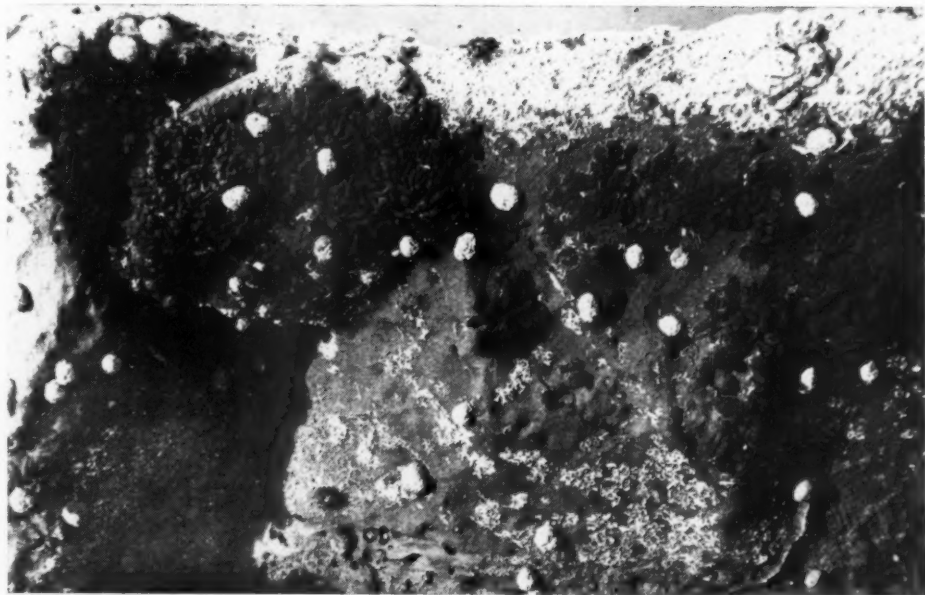


FIG. 10. *Codium adbaerens* growing above its usual level on a shaded, vertical rock face. *Chamaesipho columna* forms a white band above, *Lunella smaragda* is browsing on *Codium*, and *Vermilia carinifera* is scattered below.



FIG. 11. *Corallina*—*Hormosira* and balanoid associations on Crab Island, showing the abrupt cessation of the former with a slight increase in the level of the rock.

Nearly all of the subordinate algal species are epiphytic, chiefly because of the almost continuous covering of the substrate by the coralline turf, and most of them vary seasonally in abundance.

#### Caulerpa Clan

Within the limits of the above association, *Caulerpa sedoides* grows in isolated, cushion-like clumps between M.L.W.N. and M.L.W.S. The plant mass is so compact that other species are generally excluded, and hence the community is given the rank of clan (see p. 356).

#### 6. Encrusting Coralline Association

Vertical range: 1.7–0.2 feet. Between M.L.W.S. and 0.4 feet below E.L.W.S.

Exposure: 3–0.2 per cent.

*Corallina officinalis* (basal portion) (d)

*Peysonia atropurpurea* (f)

*Laurencia thyrsoifera* (o)

*Elminius modestus* (o)

*Melobesia* sp. (d)

*Acrosorium decumbens* (o)

*Chamaesipho columna* (o)

On most steep rock faces which descend below low water mark, a pink band of encrusting algae separates the *Corallina*—*Hormosira* association from that dominated by species of *Carpophyllum* and *Ecklonia*. The most prevalent alga here is the basal, encrusting portion of *Corallina officinalis*. Growing with it are round or oval crusts of a species of *Melobesia*, which will readily colonize other surfaces besides rock, including shells of molluscs, and even smooth pieces of glass. Intermixed with these species is a darker red, hard crust with a slimy exterior, which appears to be *Peysonia atropurpurea*. In shaded crevices, the delicate fronds of *Acrosorium decumbens* are sometimes to be found.

*Carpophyllum* and *Ecklonia* have their average upper limit (0.4 feet) in the Encrusting Coralline association. When growing at this level, holdfasts and stipes of the large brown algae may be exposed during a low

spring tide, but the fronds usually escape desiccation by trailing in the water below.

#### 7. *Mytilus*—Attached Algae Community

Vertical range: 0.7–0.2 feet. From E.L.W.S. to 0.4 feet below that level.

Exposure: 0.5–0.0 per cent.

*Mytilus canaliculus* (d)

*Caulacanthus spinellus* (1d)

*Elminius modestus* (a)

*Corallina officinalis* (d)

*Ulva lactuca* (1)

This community, which is of doubtful ecological status, is present locally where wave action is greater than usual for such a sheltered locality. It occurs at the extreme seaward end of St. Leonard's Point, both on the concrete sewer and on the rock ledges adjacent. During periods of exposure by the tide it is kept moist by surge from the constant swell or by spray if the wind is onshore. Under optimum conditions the principal dominant, *Mytilus canaliculus*, constitutes a closed community in which other members are forced to live as epiphytes on its shells. *Elminius modestus* is enabled to widen its vertical distribution in the inter-tidal region by colonizing the mussel shells.

*Mytilus* dominates in one other area—on a group of rocks outcropping from the submarine continuation of Narrow Neck Reef about 500 yards from the shore and 300 yards from the end of the Main Reef. Even on a calm day there is a considerable swell round these rocks. Associated with *Mytilus* here are dense clumps of *Ulva lactuca*, which does not occur on the Main Reef.

#### Sublittoral Brown Kelp Formation

#### 8. *Carpophyllum*—*Ecklonia* Association

Vertical range: 0.4 feet—. From E.L.W.S. to below the reach of all tides.

Exposure: 0.3–0.0 per cent.

*Carpophyllum maschalocarpum* (d)

*Carpophyllum plumosum* (d)

*Ecklonia radiata* (d)

*Carpophyllum flexuosum* (d)  
*Sargassum undulatum* (f)  
*Sargassum sinclairii* (f)  
*Cystophora torulosa* (f)  
*Ectocarpus indicus* (f) (summer)  
*Glossophora kuntzii* (la) (summer)  
*Pterocladia lucida* (l)  
*Myriogramme gattyana* (l)  
*Zonaria subarticulata* (o)  
*Cystophora retroflexa* (o)  
*Cladhymania oblongifolia* (o)  
*Acrosorium decumbens* (o)  
*Schizymenia novae-zelandiae* (r)  
*Grateloupia polymorpha* (r)  
*Myriogramme oviformis* (f) (summer)

The present account is intended to deal only with communities of the inter-tidal region; but since the dominant species in the sublittoral fringe (i.e., between 0.6 and 0.0 feet) include those of the *Carpophyllum*—*Ecklonia* association, it will be discussed here.

An association in the sublittoral region dominated by one or more species of *Carpophyllum* is characteristic of rocky districts of the east coast of New Zealand (Oliver, 1923). Narrow Neck is no exception. The only New Zealand species not present is *C. elongatum*, the chief ecological requirement of which is deep, transparent water (Cranwell and Moore, 1938). At Narrow Neck, *Carpophyllum* and *Ecklonia* are present almost everywhere within their bathymetric limits. *C. plumosum* dominates in shallower and more sheltered habitats, and is especially common on the protected western fringe of the Main Reef (Fig. 1). *C. maschalocarpum* is by far the most abundant of the three species of *Carpophyllum* in the locality. It extends almost continuously from the base of the tide pole on Crab Island, round the seaward face of the latter, and along both sides of the Main Reef (Fig. 1). In the shallower channel between reef and shore *C. plumosum* and *Ecklonia radiata* are more physiognomic. The latter is equally abundant on both eastern and western fringes of the reef. In general,

*C. flexuosum* is more typical of deeper water than *C. maschalocarpum* and *C. plumosum*, though all three flourish about A.H.B. Datum.

The upper limit of the association is remarkably constant. There appears to be a gradation in length of thallus which increases with depth at which the holdfasts are attached. This may be a response of the individual plants in connection with the optimum depth of water for photosynthesis.

A heavy epiphytic flora and fauna is supported by mature thalli of the large brown algae, and is composed mainly of diatoms, hydroids, and delicate red algae such as *Myriogramme oviformis* and *Acrosorium decumbens*. The abundance of diatoms is enhanced by the relatively slack tidal currents and the prevailing turbidity of the water.

#### Seasonal Communities

*Porphyra umbilicalis* and *Bangia vermicularis* form a winter aspect society on exposed ledges between M.H.W.N. and M.H. W.S. *Bangia* usually persists until summer.

About the level of M.L.W.N., spring and summer communities of *Myriogloia lindauerii* and *Helminthocladia australis* may be found. Both species are influenced adversely by sand.

Towards the lower limit of the balanoid association, *Splachnidium rugosum* grows in dense or isolated patches in late summer and autumn, dying away with the onset of winter.

Seasonal species do not, as a rule, reappear the following year in exactly the same situation as in the previous one.

Several points which require further commentary arise out of this discussion of the different associations:

1. The upper and lower limits given in feet represent the average for each association concerned, and do not imply that the dominant species cannot live at other levels. For instance, the lower limit of the balanoid association is 3.6



feet, but both *Chamaesipho columna* and *Elminius modestus* occur in the Encrusting Coralline association, 2 feet below.

2. Cranwell and Moore (1938) list *Lichina pygmaea* and *Melaraphe oliveri* as the chief dominants in the "supra-littoral" or "splash zone" at Narrow Neck. However, *Lichina* does not exist as a dominant here, and it has been shown from the leveling survey that *Melaraphe* does not normally occur above E.H.W.S.
3. The same association-complex is to be found with only slight local modifications farther north on Takapuna and Milford Reefs where the substrate is volcanic basalt.

#### CRITICAL LEVELS

Inasmuch as the inter-tidal region may be divided into a number of zones, each characterized by certain species which are absent or insignificant in other zones, it may be assumed that some levels are more important than others in restricting the upward or downward extension of a species. Colman (1933), David (1943), Chapman (1943), and Evans (1947) have investigated the problem of critical levels<sup>5</sup> in Great Britain, and Doty (1946) has made similar studies on the Pacific coast of North America. The fact that David found only one such level at Aberystwyth identical with one of Colman's levels at Wembury Bay, namely E.(L).H.W.N., indicates that each locality should be treated on its own merits. Both the number and the position of critical levels appear to vary from coast to coast.

From an examination of Figure 7, it is apparent that there are certain relationships between the total number of species, the num-

ber of upper and lower limits, and the level on the shore. For example, six species have their lower limits and eight species have their upper limits of vertical distribution between the levels of 9 and 12 feet, making a total of 14 limits, while only nine species occur between those levels. Between 5 and 8 feet, on the other hand, there is a total of eight limits, with the occurrence of nine species. The concept of critical levels is based on the assumption that the fewer the number of species and the greater the number of upper and lower limits at a certain level, the more critical it will be in limiting the vertical range of a species or community.

The relationship between height on the shore, number of species, and number of upper and lower limits of species was investigated from data obtained in the leveling survey. Colman's (1933) method for finding critical levels was followed. By taking from Figure 7 the number of species with limits between -1 and +2 feet, 0 and +3 feet, +1 and +4 feet, and so on, three curves were constructed (Table 2 and Fig. 12).

TABLE 2  
RELATIONSHIP OF HEIGHT ON SHORE  
AND SPECIES

FEET ABOVE OR BELOW A.H.B.D.	LOWER LIMITS	UPPER LIMITS	TOTAL LIMITS	TOTAL SPECIES	DIFFER- ENCE BETWEEN TOTAL SPECIES AND TOTAL LIMITS
+12-+15	0	1	1	1	0
11- 14	0	3	3	3	0
10- 13	1	9	10	9	1
9- 12	6	8	14	9	5
8- 11	6	7	13	10	3
7- 10	7	3	10	10	0
6- 9	5	4	9	9	0
5- 8	3	5	8	9	1
4- 7	4	3	7	8	1
3- 6	6	8	14	12	2
2- 5	10	7	17	13	4
+1- +4	11	8	19	13	6
0- +3	9	4	13	8	5
-1- +2	5	3	8	6	2

<sup>5</sup>A critical level may be defined as a level at which a relatively great number of species reach the upper or lower limit of their vertical ranges.

In Figure 12, curve A represents the number of lower limits at each level, curve B the

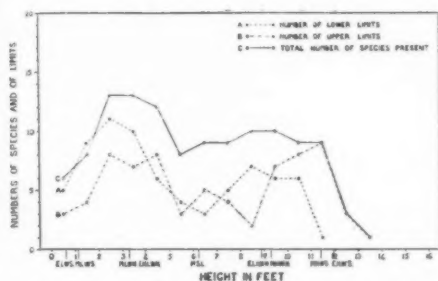


FIG. 12. Graph indicating the relationships between the number of species, and of upper and lower limits at different heights on the shore.

number of upper limits, and curve C the total number of species. There are two maxima in both A and B, one low down on the shore, and one higher up. The greatest number of both upper and lower limits occurs between +1 and +4 feet, i.e., between M.L.W.N. and M.L.W.S. (= M.L.W.M.). Curve A (lower limits) has a second pronounced maximum between 7 and 10 feet, just below E.(L).H.W.N. Curve B (upper limits) rises to a peak between 10 and 13 feet, i.e., at M.H.W.S. There is a secondary maximum at E.(H).L.W.N.

In all cases but one (between 5 and 8 feet), the total number of species is *less* than the total number of limits at any one level. At both Wembury and Cardigan Bays, however, the total number of species at each level always exceeded the total number of limits: that is, inter-tidal species in these localities have, in general, a wider vertical range than those at Narrow Neck. This difference may prove to be correlated with lower average minimum temperatures in Great Britain, associated with higher latitudes.

A further graph was constructed by plotting total limits minus total number of species against height on the shore (Fig. 13). Again there were two maxima—at M.L.W.M. and M.H.W.M.—with a subsidiary maximum between M.L.W.S. and E.L.W.S.

It is possible that these levels may be of critical significance in determining vertical

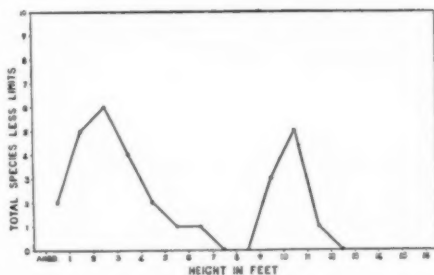


FIG. 13. Graph obtained by plotting the number of species minus the number of limits against height on the shore. The two peaks indicate the positions of two critical levels (M.L.W.M. and M.H.W.M.). M.—E.L.W.S. (between 1 and 2 feet) may also be critical.

zonation at Narrow Neck. Presumably, immediately above or below each critical level, there is a change in one or several of the factors comprising the external environment. This change must be of sufficient magnitude to restrict or inhibit optimum growth of the individuals concerned and involves a consideration of the nature of factors operating in the inter-tidal region. Investigations on the ecological factors are being continued, and it is hoped that further results will be published at a later date.

#### SUMMARY

An account is given of the plant and animal communities at Narrow Neck Reef, Auckland, in relation to their levels on the shore and to the range of exposure annually undergone by each. Four leveling traverses were made in different parts of the area to illustrate the main patterns of zonation.

The problem of critical levels is discussed. The following levels may be regarded as critical in determining zonation at Narrow Neck:

TIDE LEVEL	NUMBER OF SPECIES	NUMBER OF LIMITS	EXPOSURE per cent
I. M.L.W.S.—E.L.W.S.	8	13	1
II. M.L.W.M.	12	19	6
III. M.H.W.M.	9	14	92

The least critical level is 8.0 feet, nearly 1 foot below E.(L).H.W.N.

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## NOTES

### Translations of Japanese Botanical Papers

In the course of an investigation of the vegetation of Micronesia it became necessary to have translated a number of papers published in Japanese. To save unnecessary repetition of this work by other investigators, carbon copies of these translations, eighteen in number, have been deposited in the library of the U. S. Department of Agriculture and the Library of Congress, Washington, D. C., and in the Bishop Museum Library, Honolulu. The accompanying list gives the English transliterations of the authors' names, English translations of the titles, and the references to the periodicals in which they were published.

The translations were done under my direction by Mr. G. Luhrs Stroud, of Arlington, Va. In the especially difficult article on *Digitaria* by Tuyama, the drafts were submitted to Mrs. Agnes Chase and Mr. Jason Swallen, of the Division of Agrostology of the U. S. National Herbarium, for scrutiny and correction.

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- [Materials for a flora of Ponape, South Sea Islands]. *Kudoa* 3(4): 162-166, 1935.
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- KANEHIRA, R. [Forests of the South Seas Occupied Islands]. *Formosan Agricultural Review (Taiwan Nobizo)* 103: 17-21 (713-717), 1915.
- [Forests and plants of the South Sea Is-

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— [A plant naturalized in the South Seas]. *Journal of Japanese Botany* 18(2): 90, 1942.

— [Notes on Japanese *Digitaria*]. *Journal of Japanese Botany* 18(1): 6-21, 1942.

— "Rumphius' *Arbor ovigera*" and the related species with reference to *Hernandia sonora*. *Bulletin, Sigenkagaku Kenkyusyo* 1(1): 27-44, 1943.

Photographic copies of these translations may be secured from either the Library of Congress or from the library of the U. S. Department of Agriculture at a nominal cost.—F. R. Fosberg, *Pacific Vegetation Project, Catholic University of America.*

## News Notes

The following publications of the Natural Resources Section, General Headquarters, Supreme Commander for the Allied Powers, Tokyo, Japan, have been received. Each report includes a list of all the reports previously published, their distribution, and rules for obtaining them.

*Newsprint in Japan.* [By Harold R. Murdock.] Report No. 124. 31 pp., 9 figs., 12 tables.

*Japanese Whaling Industry Prior to 1946.* [By William M. Terry.] Report No. 126. 47 pp., 18 figs., 19 tables.

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*Oyster Culture in Japan.* [By A. R. Cahn.] Report No. 134. 80 pp., 40 figs., 17 tables.

In accordance with a recommendation of the Seventh Pacific Science Congress, a Conservation Council for Hawaii was organized at meetings held in Honolulu on July 18 and August 9, 1950. Members of the Council include representatives of approximately 25 Federal, Territorial, City-County, and private agencies and organizations. L. D. Bayer, Director of the Experiment Station, Hawaiian Sugar Planters' Association, was elected pre-

sident; H. A. Wadsworth, Dean of the College of Agriculture, University of Hawaii, vice-president; and Paul Porter, President of the Hawaii Audubon Society, secretary. The Council will operate at present through six subject committees and chairmen as follows: Land, H. A. Wadsworth; Water, C. K. Wentworth; Plants, Colin G. Lennox; Animals, Vernon E. Brock; the Sea, Col. Rollie N. Blancett; and Sites (monuments, relics, etc.), Alice Spaulding Bowen.

*The Australian Journal of Marine and Freshwater Research* has been established by the Australian Commonwealth Scientific and Industrial Research Organization, 314 Albert Street, East Melbourne, for the publication of results of original investigations on sea, estuarine, and freshwater fisheries and related subjects. The first number has already appeared, and, if sufficient material is offered, the *Journal* will be published biannually. (From the Information Bulletin of the Secretariat of the Pacific Science Association.)

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An *Advance List*, a monthly bibliography of all reports received in this field, is available for \$10.00 a year.



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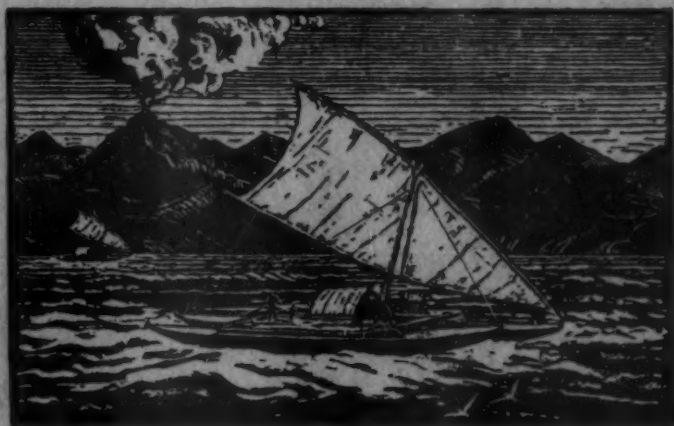
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